# BIOLOGY, STOCK ASSESSMENT AND MANAGEMENT OF THE PANGA *PTEROGYMNUS LANIARIUS* ON THE AGULHAS BANK, SOUTH AFRICA

A thesis submitted in fulfilment of the requirements for the degree of

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by

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To my family - Denis, Margie, Brian, Ian and Alistair

*Pterogymnus laniarius* (Cuvier, 1830)

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# ABSTRACT

The panga, *Pterogymnus laniarius* (Cuvier, 1830), is a South African endemic sparid fish species. On the Agulhas Bank, South Africa it is a commercially important species, caught as bycatch in the hake directed trawlfisheries and targeted by offshore hook-and-linefishers. Recently there has been considerable interest shown in directing further fishing effort on this species. The lack of a suitable management procedure for teleost bycatch in South Africa was the principal reason for undertaking this study. This thesis investigates aspects the panga's life history, particularly those aspects that have management implications. A full knowledge of this species' distribution and abundance was necessary as this could highlight the existence of any nursery areas, ontogenetic migratory patterns and areas of high spawner biomass. The derived parameter estimates were then included as inputs into stock assessment models to determine the status and productivity of the resource.

Growth studies based on sectioned sagittal otoliths revealed that the panga was a relatively slow growing fish with ages of 16 years being recorded. Growth was best described by the von Bertalanffy growth model as $L_t=379.4(1\text{-}e^{-0.13(t+1.78)})$. Total, natural and fishing mortalities were estimated at 0.36 $year^{-1}$, 0.28 $year^{-1}$ and 0.08 $year^{-1}$, respectively. Detailed histological examination of the gonads revealed that panga is a late gonochorist, males and females maturing after a non-functional intersexual stage. Females mature at approximately 200 mm fork length or 4 years of age. Reproduction occurs throughout the year although there is a slight peak in winter. Gametogenesis was found to be similar to that of other sparid fishes and marine teleosts in general. The panga feeds predominantly on crustaceans with a distinct ontogenetic shift in feeding habits. Juvenile fish feed predominantly in the water column on mysids after which they move to the benthos. Subadult fish feed principally on ophiuroids and amphipods. Adult fish remain on or near the benthos, feeding predominantly on crabs, and on polychaetes, ophiuroids and fishes to a lesser extent. Several aspects of the panga's biology contribute to its ability to sustain a higher fishing pressure than other sympatric sparid species. These include its late gonochoristic reproductive style, protracted spawning season, maturation before recruitment and preference for soft substratum prey that enables it to utilise large areas of the Agulhas Bank. The panga's longevity, slow growth and low natural mortality rate, however, mitigated against these factors and were considered in the stock assessments.

A heterogeneous Geographical Information System (GIS) was developed to analyse the distribution and abundance patterns of the panga. The GIS developed in this thesis makes a significant contribution towards the development of a South African Fisheries Information System to analyse and manage fish resources in general and bycatch resources in particular. The GIS developed in this study combines statistical Generalized Additive Modelling and standard GIS methods. Analysis of fourteen biannual fishery independent biomass surveys, disaggregated by life history stage, revealed that a nursery area for immature fish (<23 cm TL or < 4 years of age) exists on the Central Agulhas Bank. After sexual maturation, approximately 40% of the biomass migrated eastwards, colonising large areas of the Eastern Agulhas Bank. The location of the nursery area appears to be a result of the pelagic eggs and larvae being advected towards the coast in

an anti-cyclonic gyre, stemming off the Agulhas current and later deposited over the Central Agulhas Bank. The weak bottom currents on the Central Agulhas Bank prevented juvenile loss to the Benguela system. The eurytopy of adult fish to various physical variables such as temperature, dissolved oxygen and stronger currents enabled it to reduce conspecific competition and migrate eastwards with distribution primarily determined by depth. Relative biomass estimates revealed a gradual increase in biomass of 5.5% per annum between 1988 and 1995.

Predictions from yield-per-recruit, biomass-per-recruit and spawner biomass-per-recruit analyses showed that there was scope for further exploitation. A $F_{SB50}$ fishing strategy was considered to be the most appropriate fishing strategy as it did not reduce the spawner biomass-per-recruit to less than 50% of unexploited levels. Effort control was considered the most effective management tool as the age-at-50%-selectivity occurred after age-at-sexual maturity and releasing undersized fish was undesirable due to heavy mortalities resulting from severe barotrauma.

The panga resource was also assessed using an age-structured production model. The values for the free parameters of the model were estimated using biomass indices derived from fishery-independent trawl surveys. Although the data were fairly uninformative about the productivity of the resource, the results indicated robustly, that the population has recovered from low levels in the mid-1970's and could sustain higher levels of fishing intensity. Risk analysis calculations were used to assess the sustainability of different

catch scenarios. The level of sustainable catch was found to be sensitive to the selectivity pattern of the gear utilised.

Both stock assessment methods used in this study to investigate the status of the panga resource showed that the resource could theoretically sustain higher catches. It was found that although the stock could be harvested using available fishing methods, the sympatry of this species with other commercial species was of concern as the latter would form a significant bycatch in a panga directed fishery. The failure of current harvesting methods to address the bycatch problem highlights the management problem in South Africa and stresses the need for creativity by both scientists and fishers in designing new and improved methods for selectively harvesting bycatch fish resources. Considering that no suitable method is currently available to fish the panga stock in a directed fishery the fishery should be managed as *status quo* until some suitable and efficient gear is developed.

# Chapter 1 - Introduction

Fisheries management can be described as a smorgasbord of biology, mathematical statistics, economics, social science and politics. This multidisciplinary approach arises due to the economic, social and recreational values that these aquatic organisms have in the communities which exploit them. It is for this reason that the fundamental purpose of fisheries management is to ensure the sustainable management of fish stocks over time, thereby promoting the economic and social well-being of the harvesting fisheries and associated industries (Hilborn and Walters, 1992).

Since the mid 1970s, there has been a steady worldwide trend for fishery management advice to be based on more quantitative methodologies. Many of these are mathematically and statistically complex and computationally intensive (Fournier and Archibald, 1982; Deriso et al, 1985; Lewy, 1988; Schnute, 1987; Schnute et al., 1989; Punt, 1994). For South African marine resources, Punt (1992b) outlined three classes of interrelated methodologies used when providing scientific management recommendations. Primary sources of information include those methods that provide the data required for management purposes. These need to be as accurate and precise as possible, given fixed sample sizes, time and/or budget constraints. Using these synthesised data and the resultant parameter estimates, models are constructed that describe the population dynamics of the resource. These models generate most of the scientific advice used for management and include *inter alia,* estimates of the current status and productivity of the resource by applying model-estimation procedures to available data sources. Lastly, a management procedure is developed, consisting of a set of rules which, when given suitable data, can be used to provide appropriate management recommendations.

A management strategy, such as that described above would suffice for a directed fishery where data on catch, the fishing effort expended and aspects of the targeted species' biology are relatively well known. In South Africa this is the case regarding the Cape hakes *Merluccius* spp. (Punt, 1994) and Cape anchovy *Engraulis capensis* resources (Butterworth and Bergh, 1993; Butterworth et al., 1993). Problems arise, however, with those species which are not considered to be as important from a commercial perspective, due to social or economic reasons. Usually there are poor or no catch records and limited data on bycatch and discarding rates is often not available for these species. The problem is compounded by the little information on the status of these stocks and there is a general paucity of pertinent biological information.

**The bycatch problem**

Bycatch has been defined by Saila (1983) as "that part of the gross catch which is captured incidentally to the species towards which there is directed effort". A similar definition was decided on at a bycatch workshop in Newport, Oregon where the *target catch* is the species sought after by the fishery with *bycatch* comprising both the *incidental catch* of retained non-target species and *discarded catch* i.e. the portion of the catch which is returned to the sea, dead or alive due to economic, personal or legal considerations (McCaughran, 1992). These definitions are fundamentally different to those of Hall (1996) who differentiates between the *catch* which is that portion which is captured and retained and the *bycatch*, that portion which is discarded dead or is in state where death is the most likely outcome. He further divides the *catch* into two categories the *target catch* and the *non-target catch* which consists of other economically important non-target species. Within the South African demersal trawlfisheries, the catch and bycatch are both landed with discards disposed of at sea either dead or alive. Despite Hall's (1996) objectives of attempting to reduce confusion by defining terminology, he seemed to restrict himself to the bycatch of marine mammals and turtles. His new definition when seen in a South African multispecies ichthyological context is poor and needs further refinement and it is for this reason that the definition outlined by McCaughran (1992) has been adopted.

Internationally, over the past decade, there has been a rapid increase in bycatch related research. These studies have concentrated particularly on gear design (Beltestad and Misund, 1993; Broadhurst and Kennelly, 1994) and trawl efficiency devices (TEDs) (Andrew et al., 1993) to reduce incidental teleost bycatches in the Australian prawn/shrimp fishery (Andrew and Pepperell, 1992). Little work has, however, been conducted on the development of a strategy to allow for the sustainable and increased utilisation of bycatch resources as previous studies have rather concentrated on their minimisation.

Within the South African hake directed deepsea and hake and sole directed inshore demersal trawlfisheries, 12 other commercially important species are landed. These comprise 15% and 22% of the inshore and deepsea trawlfish catches, respectively (Japp et al., 1994) (Table 1.1). With increasing trends to conserve biodiversity and ecosystem functionality (Ryman et al., 1992), wastage also needs to be reduced or alternatively, utilised. Generally, with those fish species that have a low individual contribution to a fishery, there is a poor understanding of their resource status (Table 1.1). By contrast, the status of stocks with directed effort are relatively well known with assessment methods and harvesting strategies in place. As a formal management strategy to assess bycatch species is presently unavailable, the current harvesting strategies for bycatch species are *ad hoc* or at best *status-quo* (Table 1.1). For example, only if a bycatch species has similar management needs as the directed stock would it derive any management benefit. This approach is naïve and prohibits effective, sustainable management.

The development of a bycatch management strategy should, therefore, focus on various aspects of the biology of the bycatch species including its distribution and abundance, to provide some stock assessment for future management. Potential problem areas such as resource partitioning, competition for the prey of other commercial sympatric species also need to be identified. Any spatial and temporal movements such as migratory patterns and nursery areas need to be understood. These are necessary to both reduce effort on vulnerable life history stages and to identify areas of high adult density for sustainable exploitation. Using a variety of mathematical models together with available fisheries data and information from related species, or species with similar life history patterns, a sustainable level of fishing effort can be determined.

A bycatch management strategy would, therefore, need to be similar to that defined by Punt (1992b) in which the three general management methodologies he outlined are incorporated. These need to be carefully prioritised to satisfy the defined management objectives for the species under investigation.

Bycatch species in South Africa have been studied in the past using either biological (Walmsley, 1996) or biological/stock assessment (Japp, 1989; Japp and Punt, 1989; Punt and Japp, 1994) approaches. The merits of these approaches need to be evaluated as it is only possible to concentrate on various biological aspects if there is no auxiliary fishery related data on the species under investigation. Lastly, any final management recommendations made must be compatible with existing management strategies of the directed fishery of which it is a part, unless a new directed fishery is being developed for an existing bycatch species.

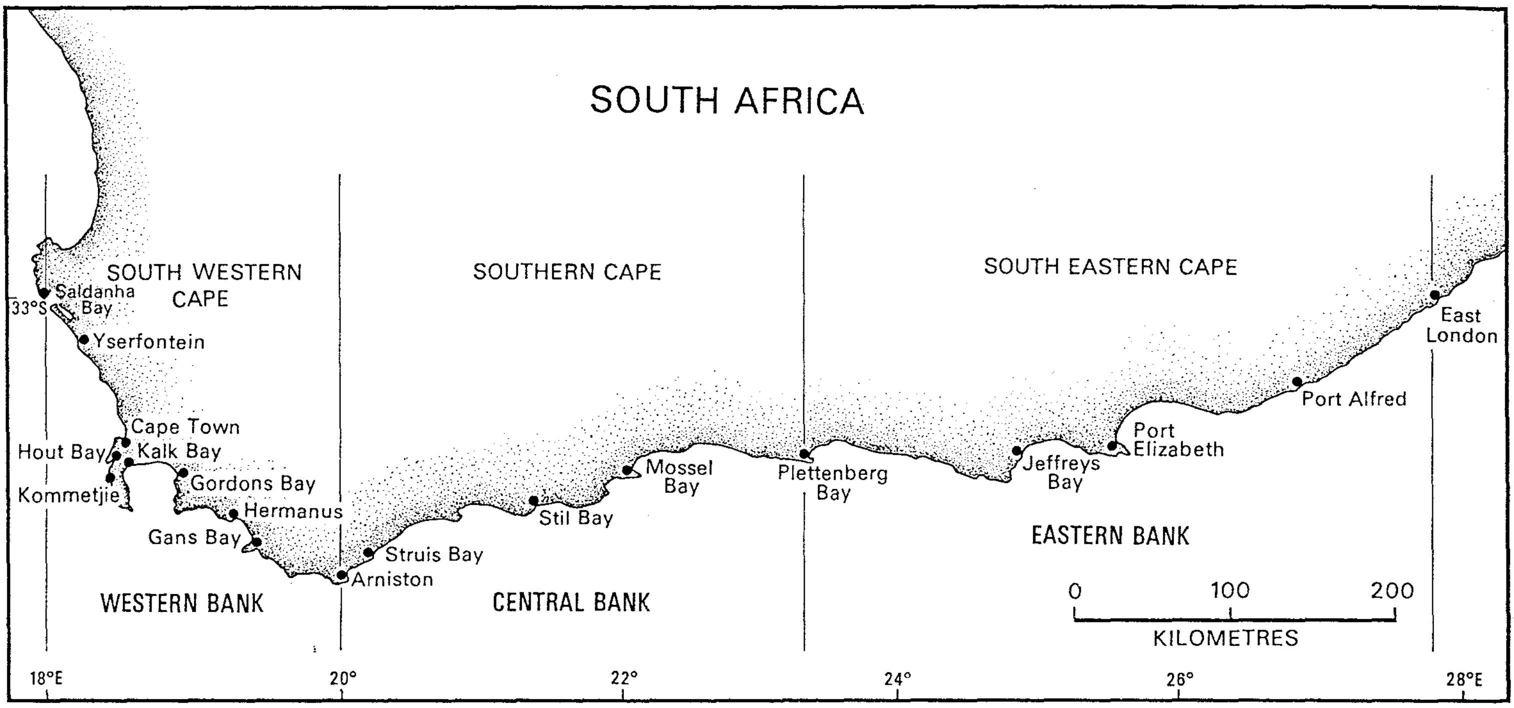

Fig 1.1. Map of the Agulhas Bank, South Africa showing the fishing ports utilised by the trawl and offshore linefisheries.

**The panga resource**

One South African bycatch species which, in the recent past, has been receiving increasing commercial interest is the panga, *Pterogymnus laniarius* (Cuvier, 1830). It is a monotypic endemic sparid species found from Namibia on the South African west coast (Botes, 1993) to KwaZulu/Natal on the east coast (Fig. 1.1) (Smith and Heemstra, 1986). It inhabits low and high profile reefs, reef-mud and reef-sand interfaces at depths ranging between 20 and 200m. It is a relatively small species attaining a maximum size and mass of 400 mm fork length (FL) and 1.5 kg respectively. It is considered to be the most abundant commercially viable sparid species on the Agulhas Bank and is caught in the recreational (Smale and Buxton,

1985) and commercial offshore hook-and-linefisheries (Hecht and Tilney, 1989) and by both the inshore and deepsea trawlfisheries (Japp et al., 1994).

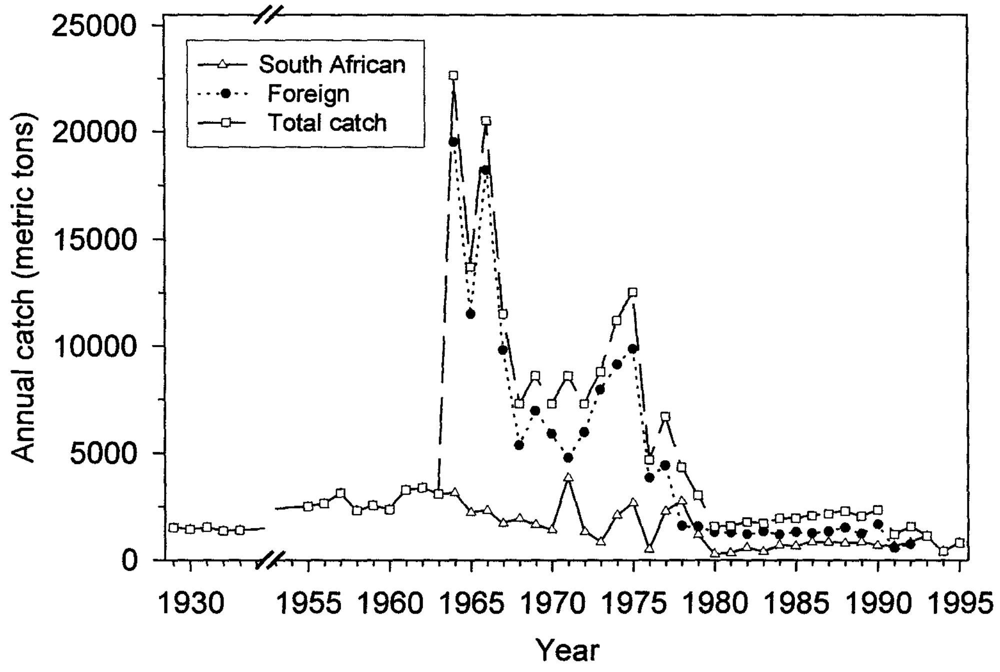

Fig. 1.2. Reported catch history of *Pterogymnus laniarius* caught on the Agulhas Bank by the South African, foreign and combined fishing fleets from 1929 to 1995.

Since the turn of the century, panga has been exploited commercially (Gilchrist, 1899; 1900; 1901; 1902; 1903; 1904). It has always been an important component of the South African fishery, and between the 1950's and the 1970's was the third most important trawlfish species landed by the South African trawling fleet (Botha, 1970; Hecht, 1976). In 1964, a directed fishery was developed for this species by Japanese and Taiwanese trawlers. These trawlers used rock hopper and bobbin trawling gear to fish the hard substrates where this species was particularly abundant. Catches peaked between 1964 and 1966 ranging between 12 000 and 18 000 *t*. During the period 1970 to 1976 catches dropped to around 8 000 *t* until the introduction of an Exclusive Economic Zone in 1978 when a quota of 1700 *t* was imposed (Crawford et al., 1987). The Japanese and Taiwanese trawlers were finally excluded from

South African waters in 1992. The reported landings of all panga caught between 1964 and 1995 are presented in Figure 1.2.

Table 1.1. Commercially important species landed within the demersal inshore and offshore trawlfisheries with comments on their perceived status and the assessment methods used in their management. Species were either caught with directed fishing effort or were caught incidentally as bycatch.

| Species | Common Name | Harvesting strategy | Status | Assessment method |
|---|---|---|---|---|
| *Argyrosomus inodorus* [1] | Silver Kob | Bycatch* | Over fished | Yield-per-recruit and spawner biomass-per-recruit |
| *Austroglossus pectoralis* [2] | Agulhas Sole | $F_{status\text{-}quo}$ | Fully fished | Virtual Population Analysis with *CPUE* data |
| *Genypterus capensis* [3] | Kingklip | Bycatch | Over fished | Age structured production model with *CPUE* data |
| *Helicolenus dactylopterus* | Jacopever | Bycatch | Uncertain | None |
| *Lepidopus caudatus* | Ribbonfish | Bycatch | Uncertain | None |
| *Lophius vomerinus* | Monk | Bycatch | Uncertain | None |
| *Merluccius* spp [4] | 2 hake species | $F_{0.2}$ | Fully fished | Dynamic production model with *CPUE* and research survey data |
| *Raja pullopunctata* | Slime skate | Bycatch | Uncertain | None |
| *Raja wallacei* | Yellowspotted skate | Bycatch | Uncertain | None |
| *Pterogymnus laniarius* [5] | Panga | Bycatch* | Uncertain | Yield-per-Recruit and Surplus production |
| *Trachurus capensis* [2] | Horse mackerel | $F_{status\text{-}quo}$ | Fully fished | Dynamic production model with *CPUE* and research survey data |
| *Zeus capensis* | Cape Dory | Bycatch | Uncertain | None |

* Also caught using directed effort in the offshore linefisheries [1] Griffiths (1997); [2] SFRI (Unpublished data); [3] Punt and Japp (1994); [4] Punt (1994); [5] Sato (1980).

Since the late 1950's the South African trawler fleet was split into two components, viz. an offshore (vessels operating deeper than 110m) and the inshore component (vessels < 30m in length and < 750 hp and restricted to an effective fishing depth of 120m). This distinction provided for better control and facilitated management. The inshore trawling fleet is smaller than the offshore component and contributes *ca.* 16% of the combined annual trawl catch (Japp et al., 1994). Over the past decade, the annual total catch of panga by all South African fishing sectors averaged 830 *t*. During this period, the percentage contribution of the panga catch to the various fishing sectors has changed (Fig. 1.3 and 1.4).

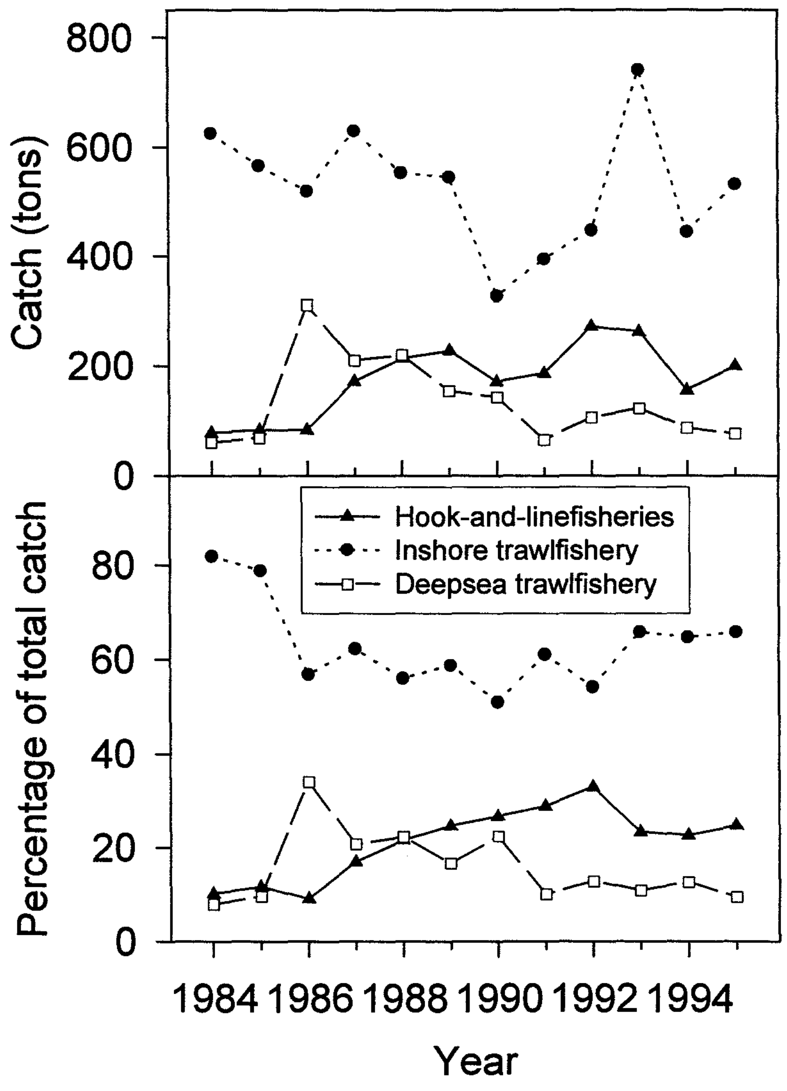

Fig.1.3. Reported landings of *Pterogymnus laniarius* by the deepsea trawl, inshore trawl and offshore hook-and-linefisheries from 1984 to 1995.

Catches by the deepsea trawl fleet have decreased whilst those in the offshore hook-and-linefishery have increased. In contrast, catches within the inshore trawlfishery have remained relatively constant.

Both trawlfisheries land approximately 80% of the annual panga catch as incidental bycatch (Figs. 1.3 and 1.4), the remainder being landed by the offshore hook-and-linefishery. The inshore trawlfishery, which operates out of Mossel Bay and Port Elizabeth, lands more than 60% of the total panga catch per annum (Figs. 1.3 and 1.4). Whilst most of the panga catch within this sector is landed at Mossel Bay, the relative proportion of panga landed to the total landings is greater in Port Elizabeth (Figs. 1.5 and 1.6). Although the proportion of panga landed by the deepsea trawlfishery is low (Figs. 1.5 and 1.6), it lands between 15 and 40% of the total annual panga catch (Fig 1.3). The noticable decline in the deepsea sector's share of the annual panga catch over the past decade reflects changes within the fishery, with effort being directed towards the deeper hake dominated grounds (>250 m) where there is a low panga density. Although panga is widely distributed along the South African coast, it is only landed by the commercial and recreational offshore hook-and-linefisheries between Kei Mouth and Cape Town. It constitutes an important component of the commercial offshore hook-and-linefish catch between Plettenberg Bay and East London (Fig. 1.5 and 1.6). Panga is not considered to be important within the recreational offshore linefishery where only 5% of the fishers target it and often use small panga as bait (Brouwer, 1997). In both sectors, panga are not a preferred species as they are small, have a low market value and are found in deeper water than other linefish species. Although only targeted by a small proportion of commercial linefishers, panga is becoming increasingly important and is currently the second most important species (numerically) landed in the commercial sector between Kei Mouth and Stil Bay (Brouwer, 1997). This trend is a consequence of the decline in abundance of other large and predominantly reef associated fish which dominated this fishery in the past (Smale and Buxton, 1985; Hecht and Tilney, 1989). No size or bag limits are currently imposed within either sector of the hook-and-linefishery.

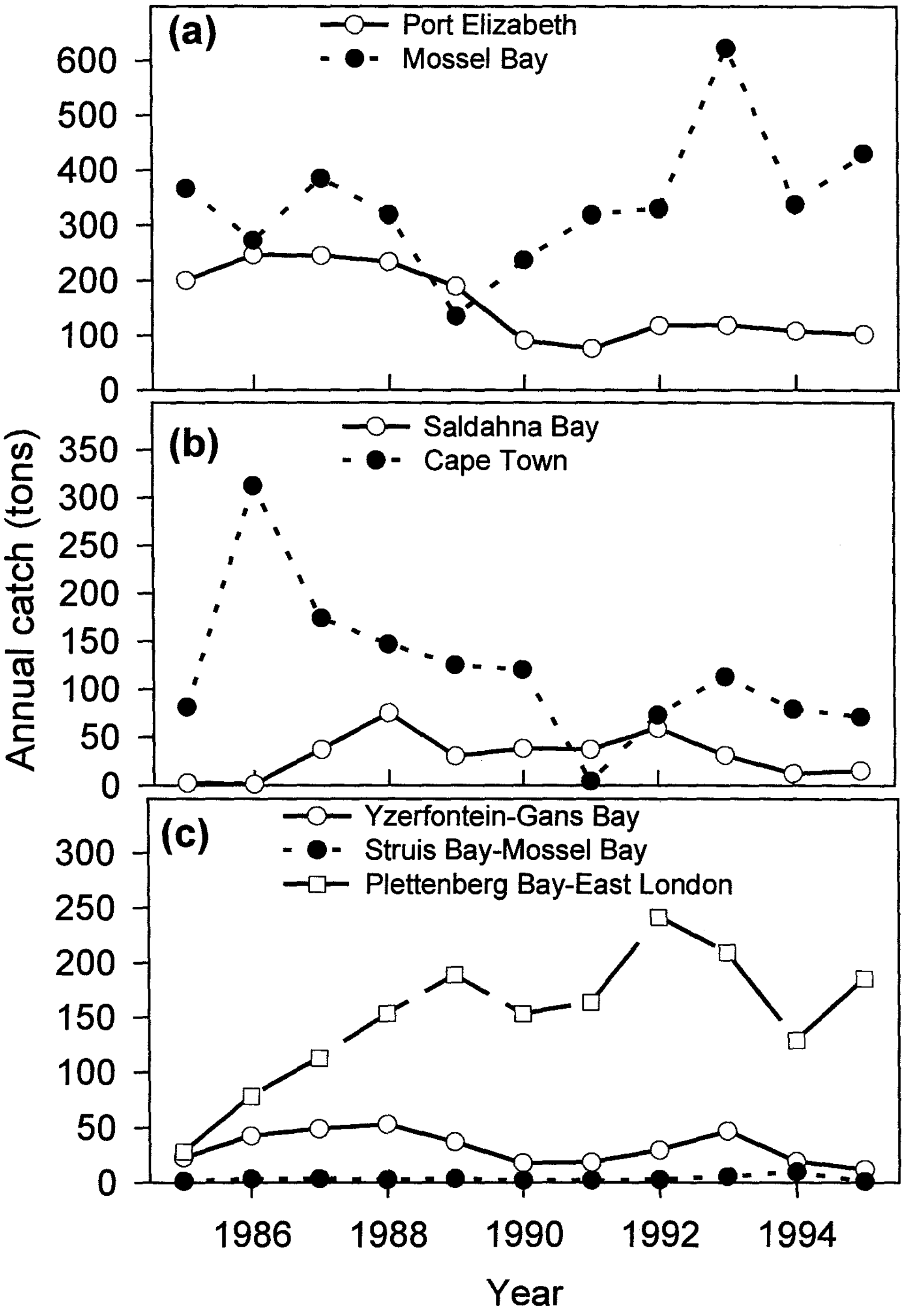

Fig.1.4. Breakdown of the catch of *Pterogymnus laniarius* by the (a) inshore trawl (b) deepsea trawl and (c) commercial offshore hook-and-linefisheries from 1985 - 1995. Catches have been summarised by geographical areas.

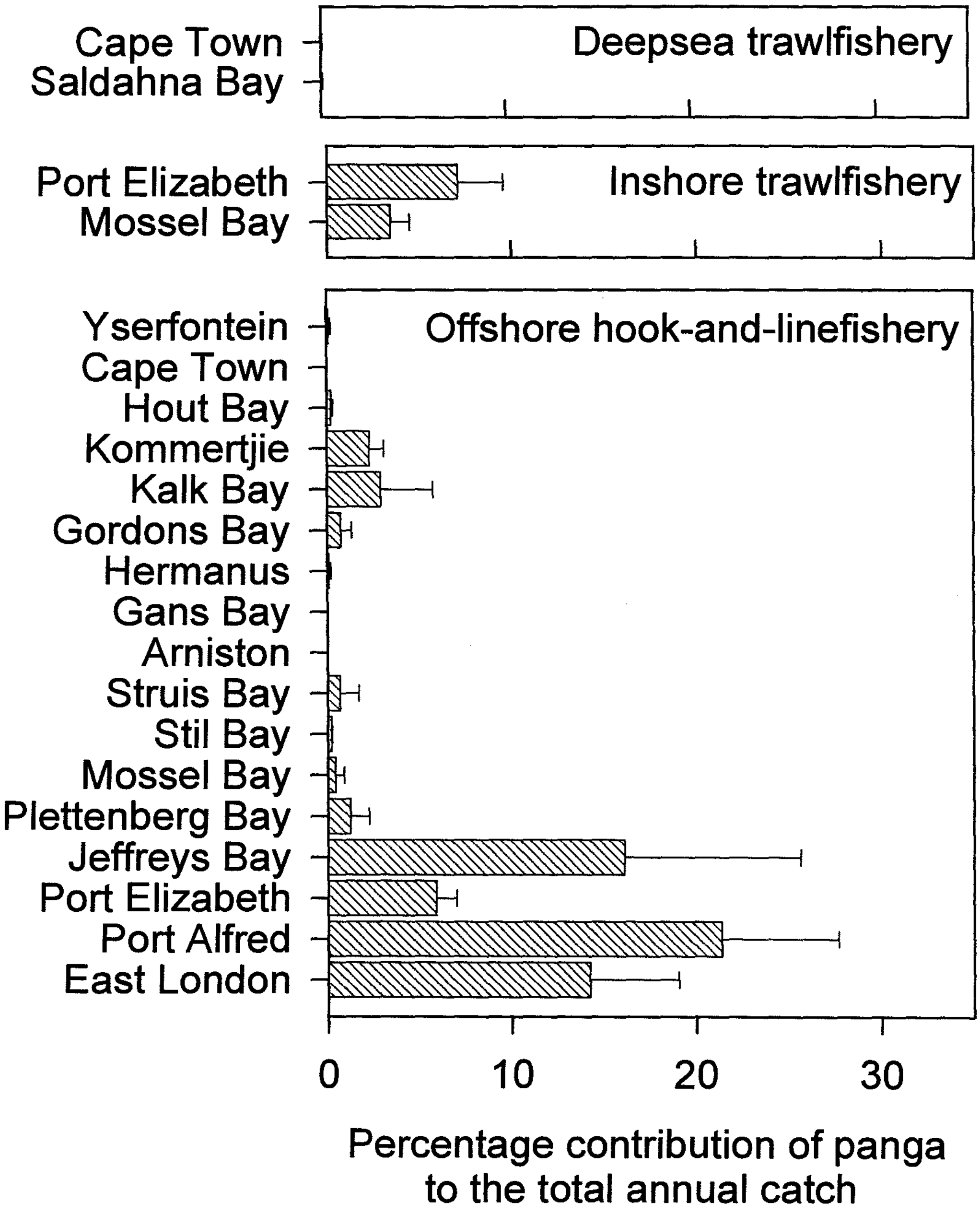

Fig.1.5. Percentage contribution of *Pterogymnus laniarius* (+one standard deviation) by mass to the total annual catch landed at various sites within three South African fishing sectors from 1990-1995.

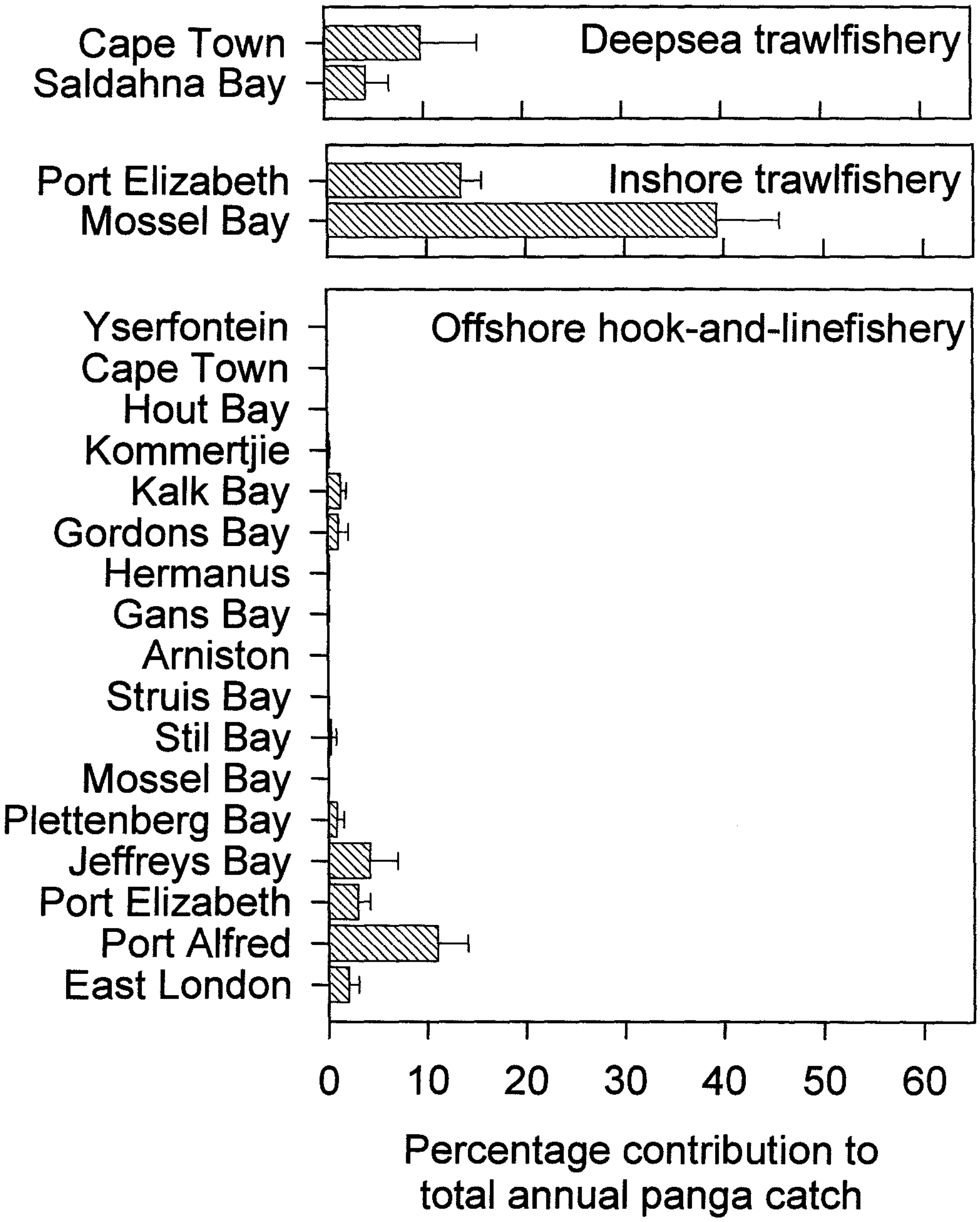

Fig. 1.6. Percentage contribution of various landing sites to the annual *Pterogymnus laniarius* catch (+ one standard deviation) within three South African fishing sectors from 1985-1995.

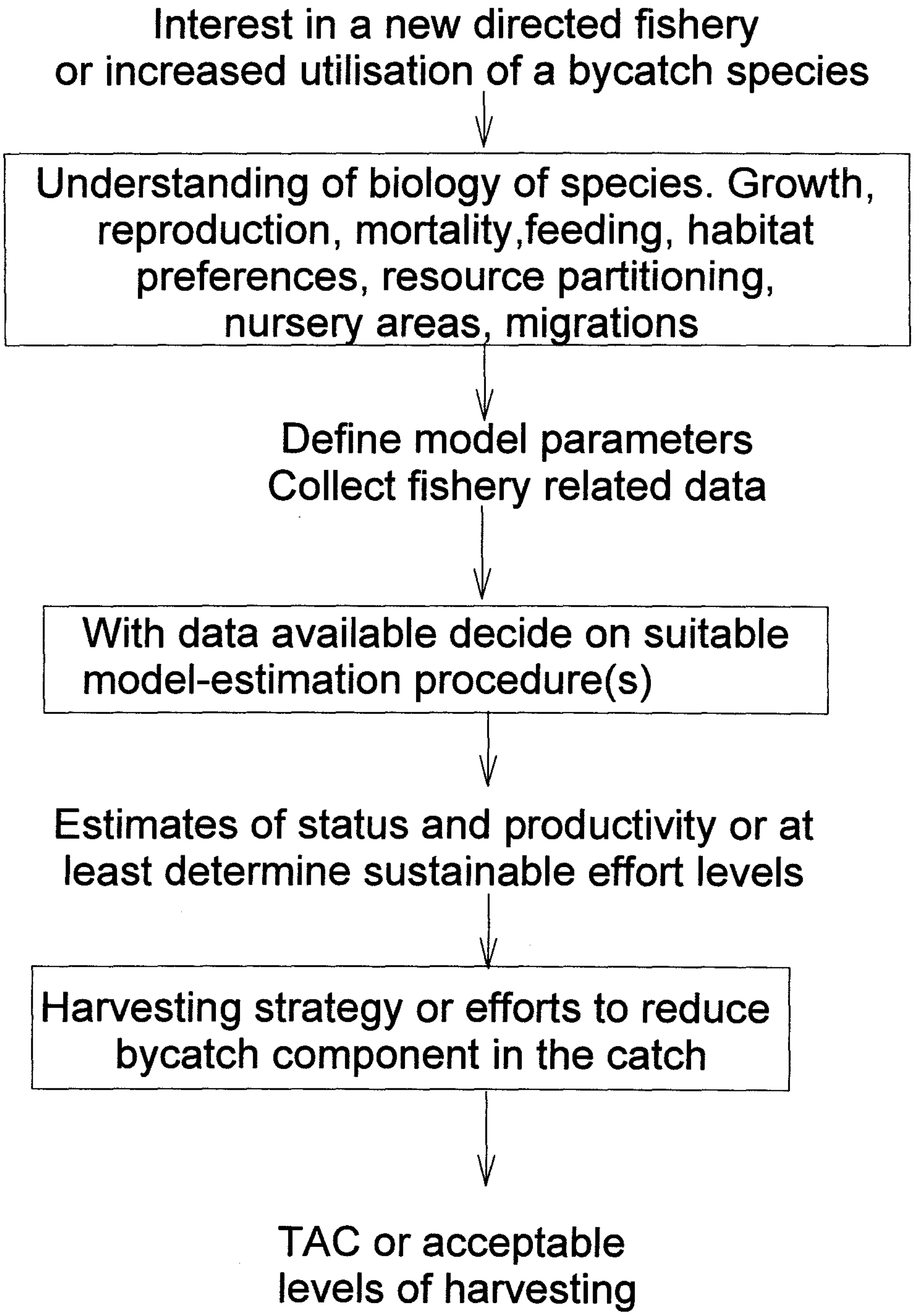

Fig. 1.7. Flow chart of a possible process leading to scientific advice on the management of a bycatch species.

### Thesis outline

This study attempts to integrate both new and existing methods to assess the biology and population dynamics of the panga resource in an effort to facilitate long-term sustainable management. The thesis is based on the flowchart in Figure 1.7, with each chapter addressing a step in the management strategy. The thesis has been divided into seven chapters. Chapter 2 describes the materials and methods used in the study, the sampling strategy and choice of sampling sites. The sources of data used in the analyses and their limitations are discussed. In Chapter 3, the biology of the panga is investigated concentrating on pertinent aspects which have implications for management, such as obtaining model parameter estimates for growth, natural and fishing mortality and size-at-sexual maturity. Chapter 4 includes a detailed analysis on the distribution and abundance of the panga stock on the Agulhas Bank. This was made possible through developing a geo-referenced, statistically robust, heterogeneous Geographical Information System. The existence of areas of high spawner biomass and nursery areas were investigated together with the estimation of relative biomass indices. The parameter estimates from Chapter 3 were used as input parameters in the models described in Chapters 5 and 6. These chapters illustrate the use of per-recruit and age-structured production models to estimate stock productivity and current stock status. Lastly, recommendations regarding the management of the resource are discussed in Chapter 7.

# Chapter 2 - Study area and sampling methods

## Study area

The Agulhas Bank is a roughly triangular shaped extension of the continental shelf south of Africa with its apex extending off Cape Infanta. It is bounded in the west by the Benguela upwelling system and in the east by the warm Agulhas Current. The Bank extends up to 300 km southwards from the African continent at its widest extremity and covers an area of 80 000 km$^2$ (Fig. 1.1), which is about one-sixth that of the North sea and twice that of the George's Bank (Schumann et al., 1988). The Agulhas Bank is a relatively nutrient-poor system, particularly in nitrate. As a consequence, there are decreased chlorophyll levels (Largier et al., 1992) and the system is less productive than upwelling dominated regions such as the South African west coast Benguela System.

The Agulhas Bank can be regarded as having primary shelf characteristics due to its width. These characteristics include having oceanographic conditions at the open ocean boundary which have little effect on temperature and circulation structures on the internal shelf region. In contrast, these regions are dominated by wind stress, tides and radiation (Lutjeharms et al., 1996; Schumann & Perrins, 1983), with the conditions on the shelf-edge boundaries being influenced by the two systems found there, the Agulhas and Benguela Currents (Boyd et al., 1985). Whilst it has been shown that the inshore coastal areas are influenced by the coastlines and its relation to the prevailing winds (Schumann et al., 1988; Schumann, 1992), the interior regions have been shown to have their own distinct circulation patterns (Swart and Largier, 1987; Largier et al., 1992).

In the past, the Agulhas Bank has been subdivided into three sub-regions namely the Western

Agulhas Bank, Central Agulhas Bank and Eastern Agulhas Bank for a variety of reasons. These sub-regions have been delineated for both descriptive purposes in biological studies (Japp et al., 1994) and for differentiating the various regions of differing primary production (Probyn et al., 1994). A recent review, which considered the nutrient characteristics of the Agulhas Bank, also recognises three sub-regions namely the Western Agulhas Bank, shelf edge of the Eastern Agulhas Bank and the Far-eastern Agulhas Bank (Lutjeharms et al., 1996). This classification is based largely on oceanographic characteristics with distinct nutrient provinces (Lutjeharms et al., 1996). The Western Agulhas Bank is largely driven by the Benguela system and derives its higher nutrient values from coastal upwelling. The shelf edge of the Eastern Agulhas Bank is under the influence of the Agulhas Current, which only contributes nutrient-poor water at the surface. The Eastern Agulhas Bank is under the influence of the Far-eastern Agulhas Bank upwelling cell, providing nutrient-rich bottom water. On the coastal boundary of the Agulhas Bank, easterly winds tend to predominate over westerly winds in summer, whilst this is reversed in winter (Schumann, 1992). These easterly winds result in cool upwelled waters flooding the adjacent coastal embayments. This is particularly prevalent off the major coast headlands off the Capes Recife, St Francis and Seal. During summer the central region of the Agulhas Bank is dominated by strong stratification and a deep mixed layer, whereas the winter storms tend to erode the thermocline, resulting in a uniformly well-mixed, deeper upper layer (Schumann and Beekman, 1984). During summer, nutrient concentrations in the surface layers are characteristic of Subtropical Surface Water, while those in the bottom water derive from Central Bank Water (Chapman and Largier, 1989).

The flow pattern on the Agulhas Bank obtained from current vector measurements between 1989 and 1991 is presented in Figure 2.1. It illustrates the strong influence of the Agulhas

Current on the Eastern Bank between Port Elizabeth and Cape Seal, with counter flows forming on the edge of the current above the 200m isobath (Lutjeharms et al., 1989). Further west, the Agulhas Current flows more directly on the edge of the Bank in the region of the Agulhas Bight before turning back onto the shelf edge above the 500m isobath. These anticyclonic flow patterns would influence pelagic biotic distribution, providing greater retainment in the Central Agulhas Bank with the flow around the cool-ridge advecting organisms inshore and eastwards (Boyd and Shillington, 1994).

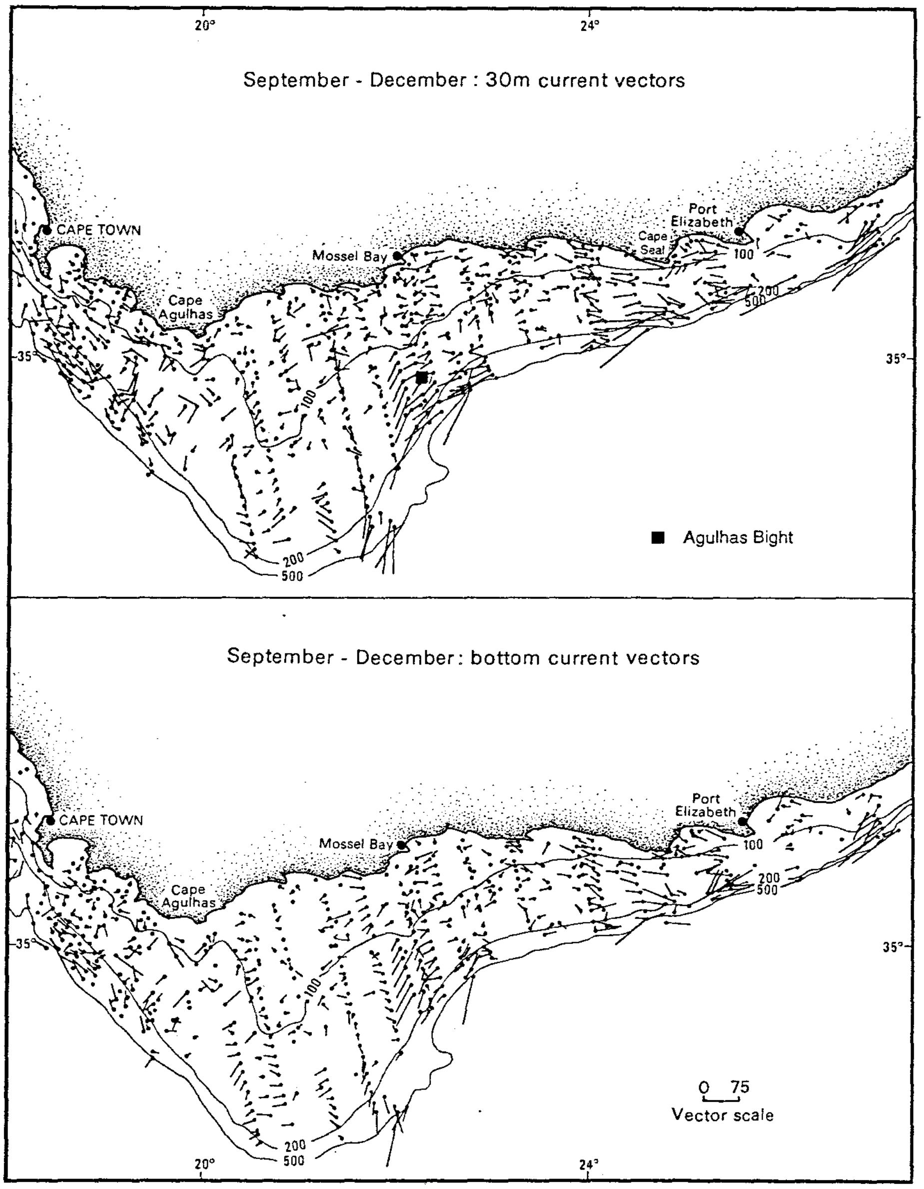

Fig 2.1. Combined ADCP current vectors for (a) 30m and (b) bottom depths collected on six survey cruises between September and November between 1989 and 1991 (redrawn after Boyd et al., 1990).

Whilst coastal wind-driven upwelling does occur, a noticeable feature of the Agulhas Bank is the a cool-upwelling ridge which extends south west from the Eastern to the Central Agulhas Bank. Various mechanisms for the forcing behind the formation of this ridge have been proposed. These include upslope veering of the bottom boundary layer of the geostrophic flow due to side-wall friction at the eastern edge of the continental shelf, and possible cross-current Ekman transport due to sustained wind stress by westerly winds on a laterally sheared flow (Swart and Largier, 1987). There is, however, no satisfactory explanation as to how the ridge is formed, its seasonality or its persistence (Boyd and Shillington, 1994).

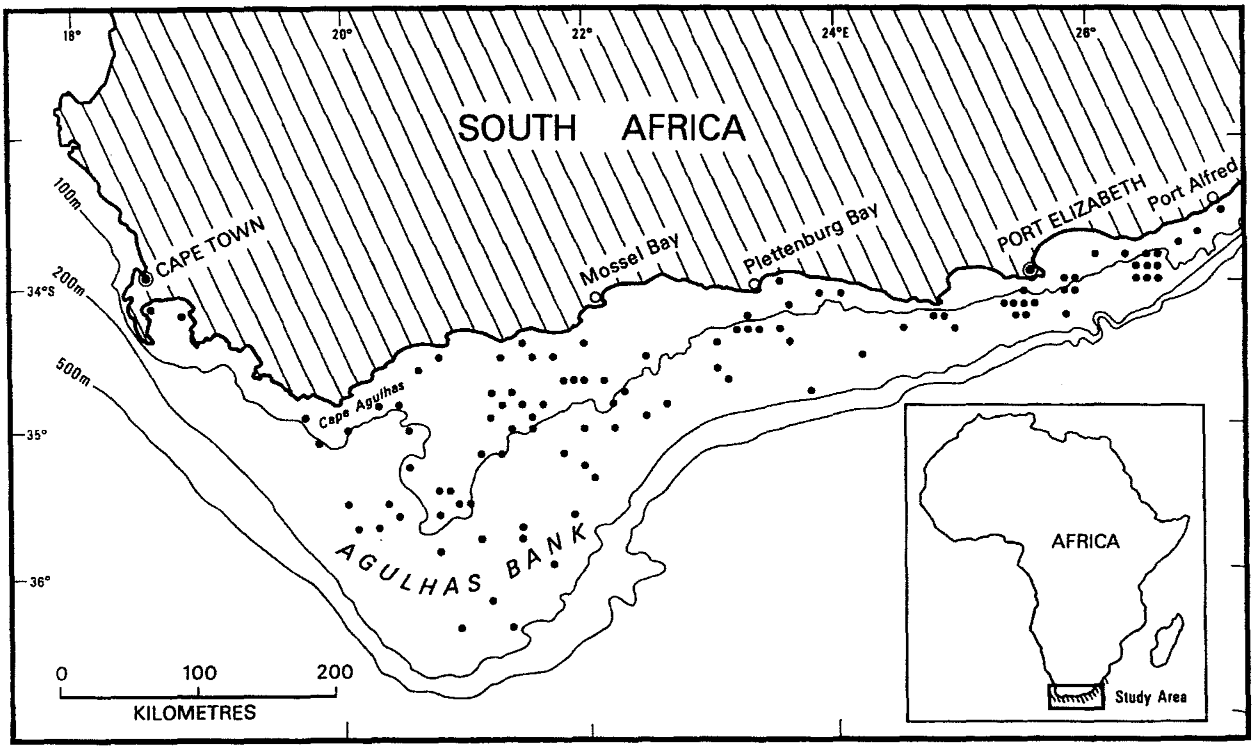

Fig. 2.2. Map of the Agulhas Bank. The hatched area denotes the distributional range of the *Pterogymnus laniarius* with the dots representing fish sampling sites

Limited quantitative sedimentological information is available on the Agulhas Bank. The sedimentological data available are, however, restricted to thematic maps (Rogers, 1971; Le Clus et al., 1994; 1996). In addition, whilst it is well known that large areas of the Agulhas Bank are comprised of low- and high-profile reef (Badenhorst and Smale, 1991), little is known about its distribution. Due to the lack of precise geo-referencing for both the reef and sedimentological data, these data were found to be unsuitable for use with the Geographical Information system developed in this study.

**Sampling methods**

The data used in this study were obtained from a variety of sources (Table 2.1). Representative samples from the inshore trawlfishery and offshore commercial hook-and-linefishery, were collected throughout most of the panga's distributional range (Fig. 2.2). These included samples of at least 30 fish per month, collected over an 18 month period between February 1994 and August 1995. Monthly samples for both length frequency and biological analysis were also obtained from the Port Elizabeth inshore trawlfishery between February 1994 and August 1995. These samples were collected on board the side-trawler *F.V. Eros,* which operated between Cape St Francis in the west and Port Alfred in the east using demersal otter trawl gear with a 75 mm stretched mesh net. Biological samples were also collected during the biannual biomass cruises on the *R.V. Africana* (April/May 1994, September/October 1994 and April/May 1995) and on one *R.V. Algoa* cruise during November 1994. These cruises were conducted between Cape Agulhas (34°50′S, 20°00′E) and Port Alfred (33°26′S, 26°54′E). Biological samples were also obtained from the linefishery operating off Port Alfred and Cape Town during February 1994 and April 1995, respectively.

A large proportion of the data, including length frequencies, biological samples and abundance indices, were obtained on the *R.V. Africana.* A brief description of the methodology used is described as follows.

Table 2.1 Sources of data used in the different analyses

| Year | Source |
|---|---|
| *Catch history* | |
| 1895 - 1904 | Gilchrist (1899-1904) |
| 1929 - 1933 | Marchand (1935) |
| 1955 - 1968 | Botha (1970) |
| 1966 - 1984 | Crawford *et al.* (1987) |
| 1985 - 1995 | SFRI, unpublished data |
| *Effort* | |
| 1985-1995 | SFRI, unpublished data |
| *Relative biomass indices* | |
| 1988-1996 | SFRI, unpublished data; This study |
| *Length frequencies* | |
| 1988-1995 (Biomass survey cruises) | SFRI, unpublished data |
| 1995-1996 (Commercial linefishery Stil Bay - Kei Mouth) | SFRI, unpublished data; This study |
| 1995-1996 (Inshore trawlfishery Mossel Bay - Port Elizabeth) | SFRI, unpublished data; This study |
| *Biological data* | |
| February 1994-August 1995 (Cape Town to Port Alfred) | This study |
| *Physical data* | |
| 1988-1995 | SFRI, unpublished data |

As previously mentioned, the Agulhas Bank area on which this study was conducted, is covered by extensive areas of reef revealed by examining the bottom profiles during the survey cruises. These areas were relatively untrawlable with conventional otter trawling gear (Badenhorst and Smale, 1991). Trawling was, therefore, confined to flat substrata to avoid damage to the gear as rock hopper/bobbins were not fitted to the foot-rope of the net.

Trawl stations were selected from a semi-randomised depth-stratified (5′ × 5′) sampling grid. Each trawl was conducted during daylight for half an hour using a 55m German otter trawl at an average speed of 3 $nm.hr^{-1}$. If a trawl was shortened for any reason, it was standardised to 30 minutes. The mouth opening of the net was 26m, surveying an area of *ca.* 0.026 nautical miles$^2$. The catch from each trawl station was identified, sorted and weighed on board and those individuals greater than 5kg weighed to the nearest 0.5 kg and smaller individuals to the nearest gramme. Length frequencies in centimeter size classes were collected for all commercial species including panga.

# Chapter 3 - The biology of the panga and its implications for management

## Introduction

In fisheries biology, the value of comparative life history studies has long been recognised. It has been shown that the life histories of similar groups of species and populations are often similar and therefore their response to exploitation can be inferred, particularly when fisheries are in the initial stages of development (Adams, 1980). As a fishery becomes developed and specific information becomes available, a more refined management strategy can be developed. Within the sparids, there are similarities in life history characteristics, particularly those with serious management implications *inter alia* sex change, longevity, slow growth, residency and barotrauma (Buxton, 1992; 1993; Buxton and Garratt, 1990). As a consequence, few sparid fishes have been shown to able to sustain high fishing pressures.

Various biological studies have been conducted on the panga in the past. Budnichenko and Dimitrova (1970) studied its age and growth using scales and its reproduction and feeding whilst Hecht and Baird (1977) investigated age and growth using whole otoliths and reproduction. Sato (1977) also aged panga using scales and Clarke and Buxton (1985) conducted preliminary feeding investigations. Aspects of its distribution and abundance have been investigated during research biomass trawling surveys (Uozumi et al., 1981; 1985; Hatanaka et al., 1983; Badenhorst and Smale, 1991; Smale et al., 1993). Unfortunately, due to the lack of histological examination of gonadal development, there is much confusion regarding its sexuality (Hecht, 1976; Uozumi et al., 1981; 1985). In addition, only whole otolith and scale based ageing methods have been conducted in past. These two methods have been shown to produce erroneous ageing results (Withell and Wankowski, 1988; Milton et al., 1995)

With the renewed commercial interest in this species and plans to target the stock, it is crucial that key aspects of its biology are comprehensively understood. Together with the nature of the previous studies which used dated methodology on limited size classes of animals it was deemed necessary to conduct a thorough investigation into its biology over the entire Agulhas Bank.

## Materials and methods

Each fish sampled was weighed (g), measured (standard, fork and total lengths) to the nearest millimeter and sexed using visual criteria (Table 3.1). The gonads were removed and weighed to the nearest 0.1 gramme. Gonadal tissues from a subsample of fish was collected monthly for histological examination of gonadal development and gametogenesis. Tissues were fixed in Bouin's solution for one week before being stored in 50% propanol. They were routinely embedded in paraffin wax, sectioned to 3-7 µm and stained using Gill's haemotoxylin and Papanicoloau's eosin A. Stomach contents were removed and preserved in a 10% buffered formalin solution. Sagittal otoliths were removed, cleaned and stored dry for later age determination. Otolith length (along the longitudinal axis), width (along the transverse axis), thickness (across the nucleus) (0.01 mm) and mass (0.001 g) were recorded from the left sagittae.

Right sagittae were lightly burned over a spirit flame to enhance growth zones. Care was taken not to char the otoliths as this tended to obscure growth patterns particularly on the margin. Burning was necessary as the otoliths were large and heavily calcified. The otoliths were embedded in clear casting resin, sectioned to 0.2 - 0.5mm through the nucleus using a double-bladed diamond saw and mounted on microscope slides with DPX mountant. Each otolith was read twice under transmitted light, approximately 2 weeks apart

Table 3.1
Macroscopic appearance and equivalent histological characteristics of *Pterogymnus laniarius* gonads at various stages during gonadal recrudescence.

| Stage | Macroscopic appearance | Histological appearance |
|---|---|---|
| 1.Virgin and resting | Ovotestis long and thin, pink in colour with no visible eggs in the ovarian element. Testicular element barely visible on the posterior edge of the ovotestis as a thin, clear ridge. | Oogonia and perinuclear oocytes in the ovary. Spermatogonia predominate in the testis. |
| 2. Developing | Ovotestis increases in size, filling half or more of the visceral cavity becoming a darker orange with grainy appearance due to visible eggs in the ovarian element. Testicular element is a small, white ridge on the posterior end of ovotestis. | Characterised by oocyte stages up to cortical alveoli stage. Testis shows all stages of spermatogenesis with undeveloped seminiferous tubules and sperm ducts. |
| 3. Active | Ovary swollen with orange-yellow and translucent eggs visible in the tissue and lumen. Testis triangular in cross-section and greyish-white in colour. Ovarian remnants visible on the testis as atrophied brown strips. | All stages of vitellogenesis present including final egg maturation. Testes show all stages of spermatogenesis and the seminiferous tubules and sperm ducts are well developed and full of sperm. |
| 4. Post-spawning | Ovary slightly flaccid with few translucent eggs visible. Brown spots are noticeable over most of the gonad. Testis becomes dirty-grey in colour and decreases in slightly in size. | All oocyte stages present in the ovary together with atretic follicles. Testis with all stages of spermatogenesis. Less sperm is visible in the sperm duct. |

If the two readings did not agree a third was taken with an age estimate accepted as the two concurrent readings. If the three readings differed by less than three years the mean of all three was taken as the age estimate, otherwise the otolith was rejected. Annulus periodicity was determined by noting the optical appearance of the otolith margin and expressing it as a percentage of the monthly sample.

Length-at-age was modelled using both the three parameter von Bertalanffy and the four parameter Schnute growth models (Ricker, 1975; Schnute, 1981). A non-parametric one-sample runs test was applied to test for randomness of the residuals and a Bartlett's test used to test for their homoscedasticity. Variance estimates were calculated using the (conditioned) parametric bootstrap technique described by Efron (1982) with 500 bootstrap iterations. The models were fitted using a non-linear minimisation routine (downhill simplex method) (Punt, 1992a) to obtain parameter estimates for the selected growth model.

Normalised age-length keys were used to transform the length-frequency distributions to age frequency distributions. Total annual mortality estimates were obtained by catch curve analysis and using the method described by Butterworth et al. (1989). Both methods were applied to the transformed age frequency data from the research and inshore trawl and commercial offshore linefish catches on the Agulhas Bank. With catch curve analysis, the negative slope of the linear regression line fitted to points greater than the age at full recruitment provided an estimate of instantaneous total mortality ($Z$). The second method described by Butterworth et al. (1989) is considered to be statistically superior to the catch curve analysis if the numbers caught at any age are low. This mortality model is described by the equation

$$Z = ln\ [1 + \frac{1}{(\bar{a}\ -\ a_f)}]$$

where $a_f$ is the age at full recruitment and $\bar{a}$ the mean age of all fully recruited fish. Natural mortality ($M$) was estimated using both the Pauly (1980) equation

$$\text{Log}\ M = -\ 0.0066 - 0.279\ \text{Log}\ L_\infty + 0.6543\ \text{Log}\ K + 0.4634\ \text{Log}\ T$$

and the Rikhter and Efanov (1977) equation

$$M = [\frac{1.521}{t_m^{0.72}}] - 0.155$$

where $T$ is the mean temperature (°C), $L_\infty$ and $K$ are von Bertalanffy parameters and $t_m$ the age-at-maturity. Fishing mortality was obtained by substitution ($F = Z - M$). The mean annual water temperature in the study area was 12°C (M. Roberts, Sea Fisheries Research Institute, Unpublished data).

Size at sexual maturity was calculated by fitting a logistic ogive to the proportion of reproductively active female fish (active and post-spawning) during the spawning season in centimeter size classes. The two parameter logistic ogive is described by the equation

$$P(L) = \frac{1}{1 + e^{-(L-L_{50})/\delta}}$$

where $P(L)$ is the percentage of mature fish at size $L$, $L_{50}$ the length-at-sexual maturity and $\delta$ the width or steepness of the ogive. The model parameters were estimated by minimising the squared difference between the observed and predicted maturity values. A gonadosomatic index was calculated for mature fish by expressing gonad mass as a percentage of eviscerated body mass. Adult sex ratio was determined using fish larger than the length at maturity, with mature intersexual fish classed according to the dominant, macroscopically visible gonadal tissue. Later histological validation showed that this closely approximated the functional sex of mature fish.

Prey items contained in each stomach were sorted into groups, identified to the lowest possible taxon and quantified in terms of frequency of occurrence and visual percentage volume (Berg, 1979). Numerical abundance could not be accurately quantified as prey items were masticated. Each prey group was assigned a rank computed as the frequency of occurrence multiplied by the mean percentage volume (Hobson, 1974).

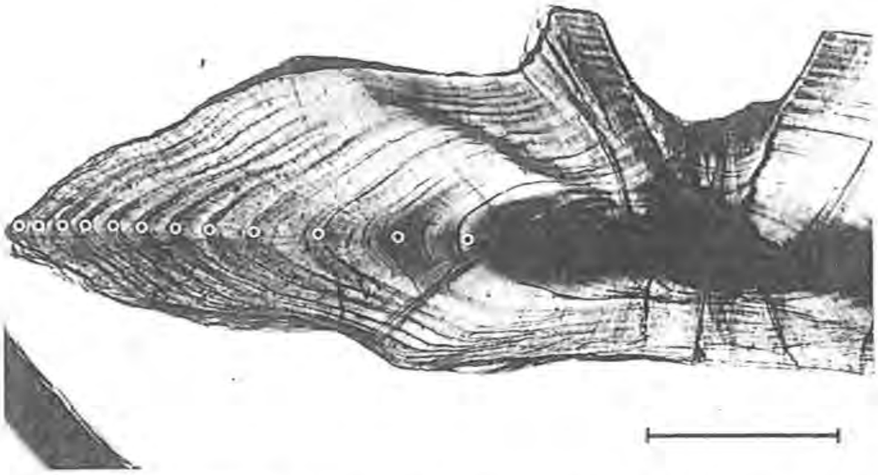

Fig. 3.1. Photomicrograph of a sectioned sagittal otolith of a 12-year old *Pterogymnus laniarius* viewed with transmitted light. Scale bar = 1mm.

## Results

### *Age and growth*

Morphometric relationships between length and weight and otolith length, diameter, mass and width are summarised in Table 3.2. Alternating opaque and translucent zones were easily visible in most otoliths (Fig. 3.1) with the otoliths of fish up to 8 years of age being easily interpreted. Due to the lack of differentiation in opaque growth zones caused by the progressive decrease in width of the adjacent translucent zones, age interpretation became difficult in older fish. The change in growth zone deposition after 8 - 10 years was an area of concern. Few of the otoliths of old fish sampled showed signs of stacking which is a common otolith growth pattern in long-lived sparids where the growth zones of the otoliths become deposited vertically rather than horizontally (Buxton and Clarke, 1991; 1992; Mann, 1992). In panga otoliths, the growth zones continued to be deposited horizontally with the translucent zones becoming progressively narrower with age. This resulted in the opaque zones merging into one another with annuli interpretation becoming increasingly difficult in older fish. Of the 668 otoliths read, 53 were rejected as unreadable. Growth parameters were determined using 352 otoliths with the remainder being used to construct an age-length key. Marginal zone analysis on fish up to 10 years of age showed that an opaque zone was deposited each year during the winter months, between June and September (Fig. 3.2). Based on this it was assumed that each opaque zone represented an annulus and one years growth comprised of an opaque and it's adjacent translucent zone.

Table 3. 2
Morphometric relationships for *Pterogymnus laniarius* sampled on the Agulhas Bank between February 1994 and July 1995.

| | Relationship | *n* | $r^2$ |
|---|---|---|---|
| Total mass (g) | = 0.00002 Fork length (mm) $^{3.031}$ | 1460 | 0.99 |
| Eviscerated mass (g) | = 0.00002 Fork length (mm) $^{3.023}$ | 1706 | 0.99 |
| Fork length (mm) | = 1.126 Standard length (mm) + 4.8005 | 1390 | 0.99 |
| Fork length (mm) | = 0.901 Total length (mm) - 0.6848 | 1390 | 0.99 |
| Fork length (mm) | = 15.811 Otolith length (mm)$^{1.119}$ | 613 | 0.98 |
| Fork length (mm) | = 20.963 Otolith width (mm) $^{1.133}$ | 613 | 0.97 |
| Fork length (mm) | = 106.04 Otolith thickness (mm) $^{0.852}$ | 613 | 0.92 |
| Fork length (mm) | = 440.26 Otolith mass (g) $^{0.394}$ | 613 | 0.97 |

No significant difference between the von Bertalanffy and Schnute growth models was found using a likelihood ratio test ($F = 0.77$; $df = 2{,}349$; $p > 0.05$) (Draper and Smith, 1966). Due to fewer parameters, the relationship between length and age was best described by the three parameter von Bertalanffy model (Tables 3.3 and 3.4, Fig. 3.3). There was no significant difference in growth rates between males and females using a likelihood ratio test ($F = 1.71$; $df = 2, 591$; $p > 0.05$). A summary of previous age and growth studies conducted on the panga is summarised in Table 3.5.

*Mortality*

Age-frequencies derived from length frequency data collected from research and commercial vessels provided estimates of total mortality (Fig. 3.4, Table 3.6). Fish first entered both the trawl and linefisheries at 4 years of age and were fully selected by 5.5 and 7.3 years of age in the two fisheries, respectively. Total mortality estimates obtained from both the catch curve analysis and Butterworth et al. (1989) methods using research trawl data were slightly higher than the estimates obtained from both commercial fisheries. Overall, there was little difference between the estimates and a first approximation of total mortality was obtained by averaging all the estimates at 0.36 year $^{1}$.

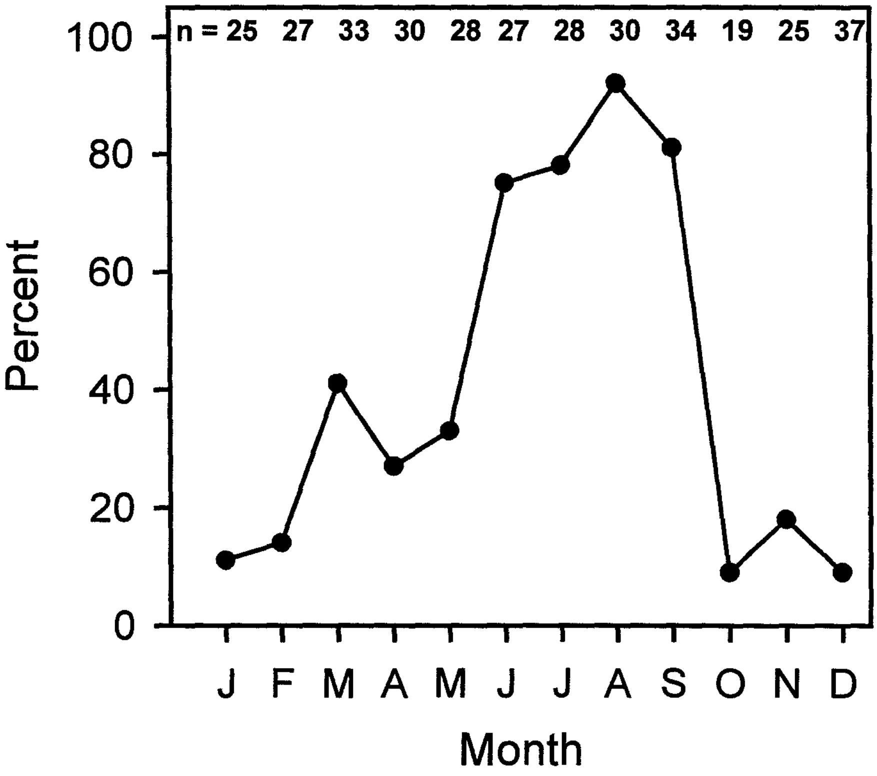

Fig. 3.2. Percent of *Pterogymnus laniarius* otolith samples with an opaque margin, sampled monthly on the Agulhas Bank between February 1994 and July 1995. n = number of otoliths analysed per month.

Intuitively, with an annual catch of <2% of the standing stock over the past decade, fishing mortality should be expected to be extremely low with the resultant estimate of natural mortality approximating total mortality. The two empirical estimates of natural mortality obtained were both found to be unsuitable. Pauly's (1980) estimate of 0.16 year$^{-1}$ was considered to be most accurate of the two empirical methods investigated. It was, however, considered to be too low whilst Rikhter and Efanov's (1977) estimate 0.40 year$^{-1}$ was higher than the total mortality estimate. It was for this reason that an average of the two estimates 0.28 year$^{-1}$, was taken as a first approximation of natural mortality and by substitution fishing mortality was calculated as 0.08 year$^{-1}$.

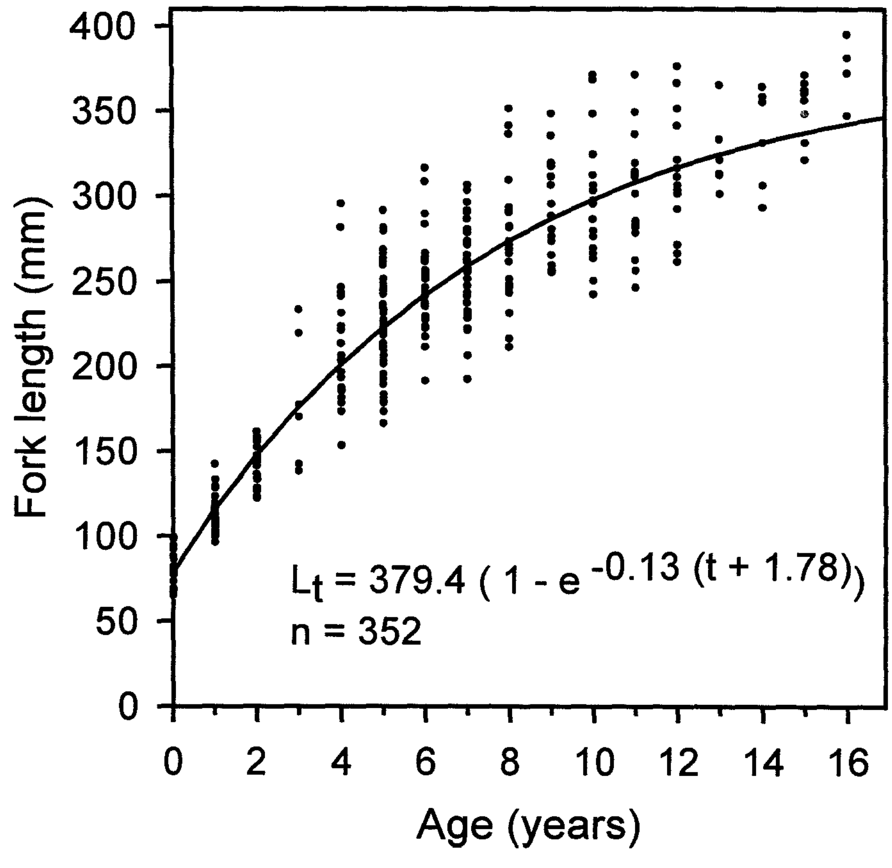

Fig. 3.3. Observed individual lengths-at-age of *Pterogymnus laniarius* using sectioned sagittal otoliths. Samples were collected on the Agulhas Bank between February 1994 and July 1995.

*Reproductive biology*

In the panga, gonads are typically cystovarian and suspended by a dorsal mesentery in the posterior region of the visceral cavity. In general, both gonadal lobes were equally well developed, although occasionally one was reduced. The length frequencies of the sexes of the panga sample are shown in Figure 3.5. Macroscopical and histological appearances of the gonads were different. Macroscopically, gonad development appeared to proceed in a female direction after an initial juvenile stage which appeared to be ovarian. Males appeared in the population after an intersexual stage which was recognised if there was any evidence of an intersexual gonad regardless of the size or stage of each component tissue.

Histological examination revealed a different pattern with the early ontogeny of all gonads sampled being intersexual. These gonads were dominated by ovarian tissue with a very small testicular element containing spermatogonia on the posterior lateral edge (Fig. 3.6a) which was invisible macroscopically. The testis became visible macroscopically at 17cm FL as a small clear ridge situated on the lateral posterior margin of the ovotestis.

Table 3.3
Growth model parameter estimates for *Pterogymnus laniarius* using both the von Bertalanffy and Schnute growth models. Models were fitted using a relative error structure to observed length-at-age data sampled on the Agulhas Bank from February 1994 to July 1995. $n$ = 352.

| Parameter | Estimate | Standard error |
|---|---|---|
| | von Bertalanffy model | |
| $L_\infty$ | 379.35 | 13.82 |
| $K$ | 0.13 | 0.01 |
| $t_0$ | -1.78 | 0.10 |
| | Schnute model | |
| $t_1$ | 0 | - |
| $t_2$ | 16 | - |
| $l_1$ | 79.72 | 2.05 |
| $l_2$ | 331.19 | 9.11 |
| $a$ | 0.21 | 0.06 |
| $b$ | 0.40 | 0.44 |

Table 3.4
Mean observed (± standard deviation) and expected fork lengths-at-age of *Pterogymnus laniarius* sampled on the Agulhas Bank between February 1994 and July 1995. Expected values are from the von Bertalanffy model with a relative error structure.

| | | Fork length (mm) | | |
|---|---|---|---|---|
| Age (years) | *n* | Range | Observed | Expected |
| 0 | 22 | 64-98 | 80.6±10.1 | 78.4 |
| 1 | 24 | 95-141 | 112.9±10.97 | 115.1 |
| 2 | 21 | 121-141 | 141.9±12.9 | 147.3 |
| 3 | 6 | 137-232 | 178.8±39.1 | 175.6 |
| 4 | 27 | 152-294 | 209.4±6.2 | 200.4 |
| 5 | 62 | 165-290 | 228.0±28.9 | 222.3 |
| 6 | 38 | 190-315 | 248.5±24.3 | 241.4 |
| 7 | 35 | 191-305 | 256.8±29.1 | 258.2 |
| 8 | 29 | 210-350 | 268.7±35.2 | 273.0 |
| 9 | 17 | 254-347 | 288.1±29.1 | 286.0 |
| 10 | 17 | 241-370 | 296.3±38.1 | 297.4 |
| 11 | 17 | 245-370 | 304.3±35.8 | 307.4 |
| 12 | 16 | 260-375 | 312.7± 33.2 | 316.1 |
| 13 | 7 | 300-364 | 329.0± 25.8 | 323.9 |
| 14 | 6 | 292-363 | 333.5± 29.6 | 330.6 |
| 15 | 8 | 320-370 | 350.9± 17.5 | 336.6 |
| 16 | 3 | 346-394 | 372.8± 20.2 | 341.8 |

Table 3.5
Comparison of von Bertalanffy growth parameters for *Pterogymnus laniarius* obtained using different methods sampled from various areas of the Agulhas Bank between 1968 and 1995.

| Source | Method | Area | Ages | $K$ | $t_0$ | $L_\infty$ cm |
|---|---|---|---|---|---|---|
| Budnichenko and Dimitrova (1970) | Scales | Whole[1] | 1-12 | 1.66[3] | -1.73[3] | 61.4FL[3] |
| Hecht and Baird (1977) | Whole otoliths | East[2] | 2-11 | 0.19 | -0.32 | 42.7FL[4] |
| Sato (1977) | Scales | Whole[1] | 1-13 | 0.18 | -0.33 | 38.3FL |
| This study | Sectioned otoliths | Whole[1] | 0-17 | 0.13 | -1.78 | 37.9FL |

Max. Age = Maximum age; $K$, $t_0$, $L_\infty$ the von Bertalanffy growth parameters; [1]20-27°E; [2]24-27°E; [3] von Bertalanffy parameters were calculated from published mean lengths-at-age; [4] Equivalent to 48.1mm TL

Table 3.6
Total ($Z$), natural ($M$) and fishing ($F$) mortality estimates obtained for *Pterogymnus laniarius* sampled on the Agulhas Bank between 1993 and 1994. Total mortality was estimated from samples collected using research and commercial inshore trawl fishery otter trawl gear and commercial offshore linefishing gear. The estimate of $M$ is an average of both Pauly (1980) and Rikhter and Efanov (1977).

| Method | Z (Catch Curve) | Z (Butterworth et al.) | Z (Average) | M | F |
|---|---|---|---|---|---|
| Research trawl | 0.38 | 0.38 | 0.38 | 0.28 | 0.10 |
| Inshore trawlfishery | 0.35 | 0.35 | 0.35 | 0.28 | 0.07 |
| Offshore linefishery | 0.33 | 0.38 | 0.36 | 0.28 | 0.08 |
| Averaged estimate | 0.35 | 0.37 | 0.36 | 0.28 | 0.08 |

Ovarian and testicular elements were separated by connective tissue, a typical sparid pattern (Atz, 1964). Later, this connective tissue split, giving rise to the formation of sperm ducts (Fig. 3.6b).

Two developmental pathways were evident before sexual maturation. Either the volumetric increase in the size of the ovarian element resulted in a functional female or the continued development of the testicular element and simultaneous atresia of the ovarian element resulted in a functional male (Fig. 3.6c). In functional males, the ovarian element was only evident as atretic previtellogenic oocytes lining a rudimentary oviduct (Fig. 3.6d). As sexual differentiation slightly preceded sexual maturity, many functional females had evidence of the latent sex with a small testicular element present (Fig. 3.6e). However, in the majority of individuals the sperm ducts were undeveloped or were void of sperm. With further ovarian development the testicular element ceased spermatogenesis consisting of spermatogonia (Fig. 3.6f). Despite this overall pattern, there were a few individuals that appeared to be simultaneously functional males and functional females but were not restricted to a particular size class. These results, therefore, indicate that the panga is a late gonochorist (= rudimentary hermaphrodite *sensu* Buxton and Garratt, 1990). A schematic representation of gonadal development is outlined in Figure 3.7.

The classification of oocyte development was based on criteria used by Wallace and Selman (1981), Coetzee (1983) and Buxton (1990). Despite differences in the number of egg stages quoted by the various authors, two principal phases described by Buxton (1990) were identified, pre-vitellogenesis resulting from oogonia to the end of the perinuclear stage and vitellogenesis from the primary vesicle oocyte stage to final egg maturation.

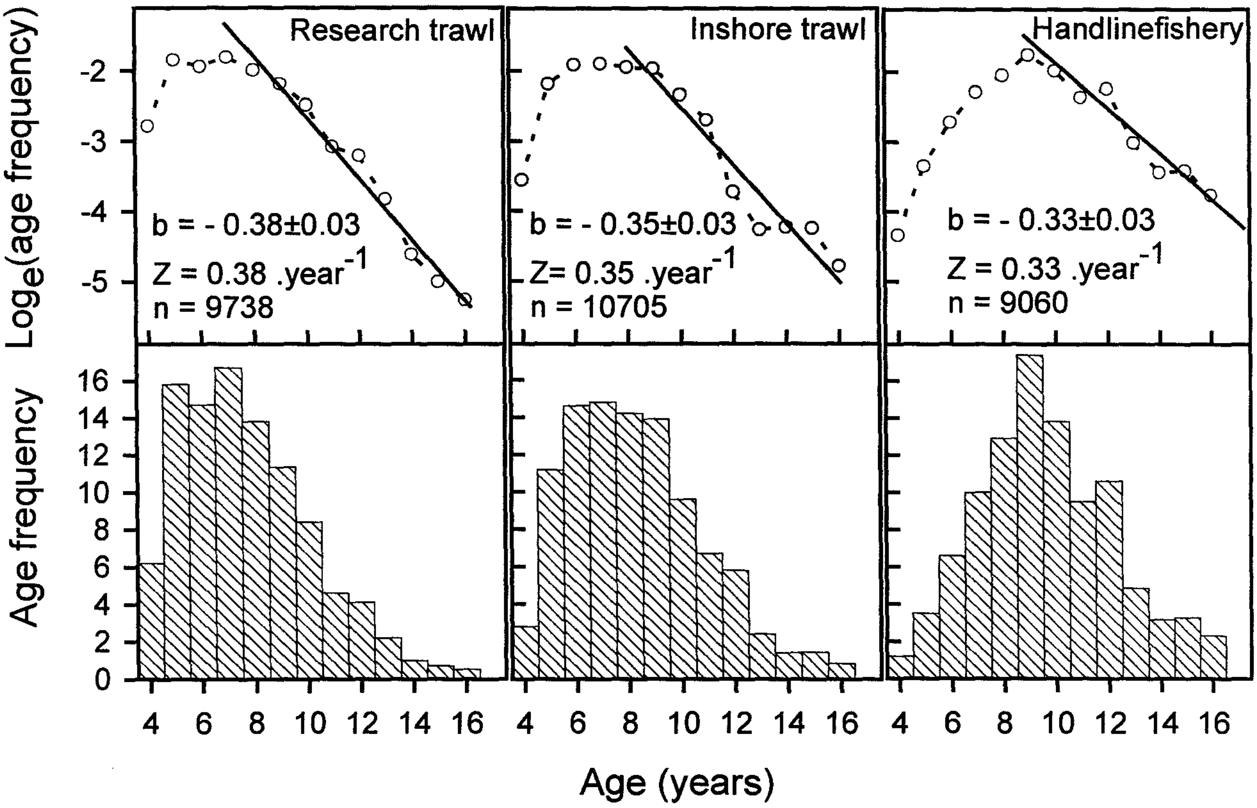

Fig. 3.4. Age-frequency distributions and catch-curves of *Pterogymnus laniarius* sampled using three gear types on the Agulhas Bank between 1993 and 1994.

Oogonia were most frequently observed at the periphery of the ovigerous lamellae embedded in the germinal epithelium. They are characterised by their small size, large nucleus to cytoplasm ratio and lightly basophilic cytoplasm.

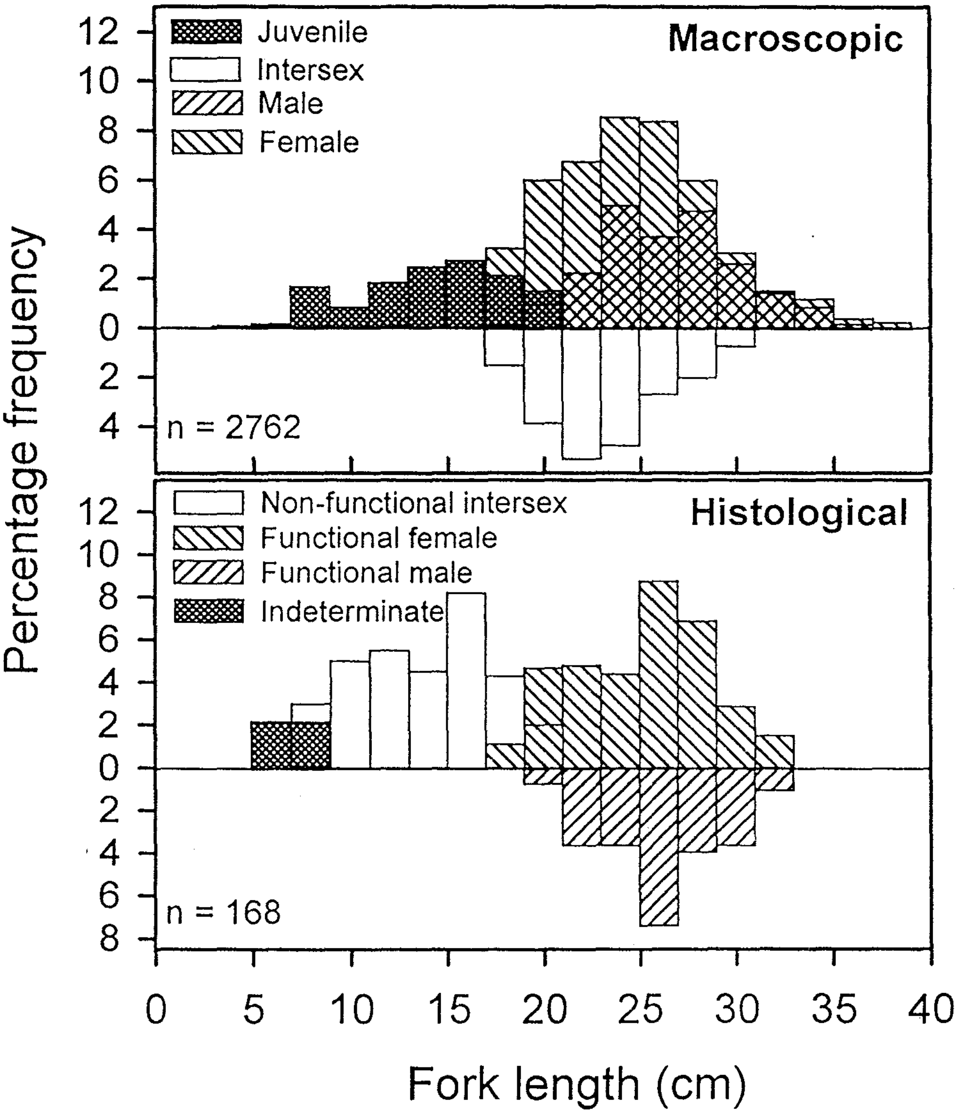

Fig. 3.5 . Size frequency histograms of *Pterogymnus laniarius* sampled during research cruises on the Agulhas Bank between May and October 1994 determined both macroscopically and histologically. Note that macroscopic stageing does not imply sexual functionality. Macroscopically, an intersexual gonad merely notes the co-occurrence of ovarian and testicular tissue whilst histologically it denotes an immature intersexual gonad.

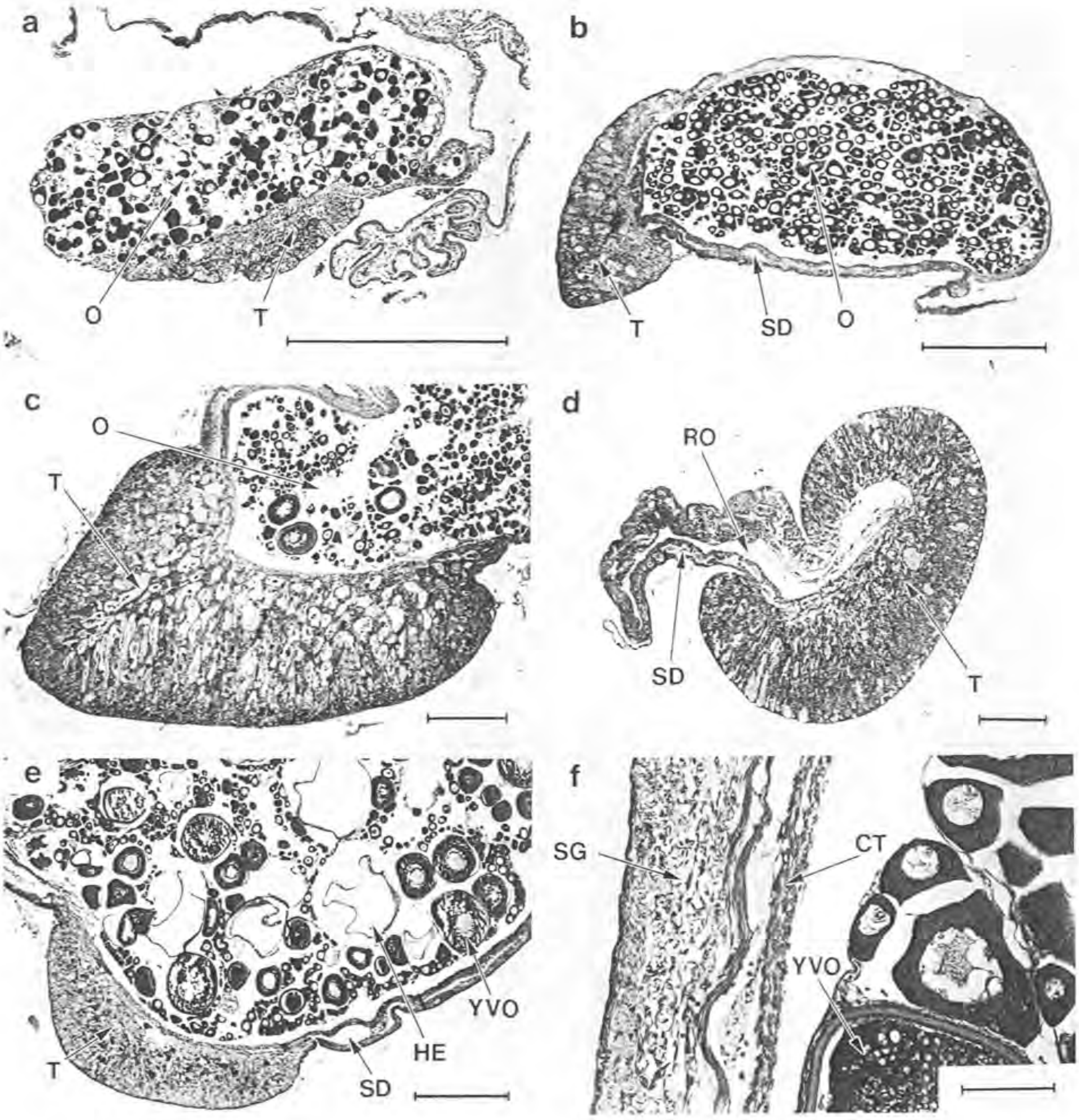

Fig. 3.6. Transverse sections through *Pterogymnus laniarius* gonads illustrating gonadal development. (a) The ovotestis of a juvenile fish (125 mm FL) showing the testicular element (T) clearly separated from the ovarian element (O). (b) The ovotestis of an immature fish (206 mm FL) just prior to sexual differentiation. Note the development of the sperm duct (SD) and the layer of connective tissue separating the ovarian and testicular elements. (c) Ovotestis of a functional male (250 mm FL) showing the simultaneous growth in the size of the testis and the degeneration of the ovary with oocytes in the cortical alveoli stage of development. (d) A mature testis (278mm FL) exhibiting the remains of the ovarian element surrounding a rudimentary oviduct (RO). The sperm ducts are full of sperm. (e) Ovotestis of a functional female (277mm FL) with a testicular remnant. Note the lack of spermatogenesis and empty sperm ducts. YVO = Yolk vesicle oocyte, HE = Hydrated egg. (f) Testicular remnant of a functional female. Testis consists entirely of spermatogonia. CT = Connective tissue. Scale bars a-e = 600 mm; f = 100 mm. Stained using Gill's Haemotoxylin and Papanicoloau's eosin A.

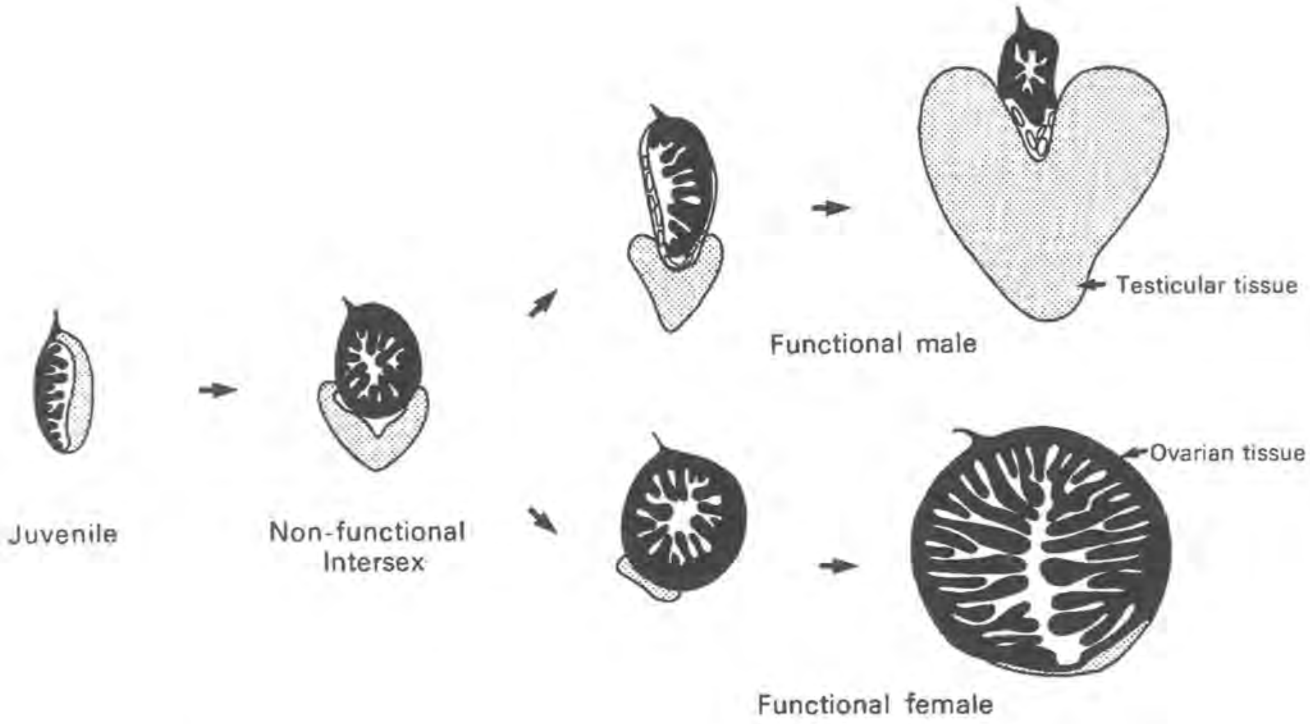

Fig. 3.7. A schematic representation of gonadal development in *Pterogymnus laniarius*.

With the initiation of the first meiotic division and further growth, perinuclear oocytes appear (Fig. 3.8a). They are strongly basophilic, have numerous nucleoli and a well defined thecal covering. Pre-perinuclear oocytes are polygonal in shape with an intensely basophilic cytoplasm and are found closest to the germinal epithelium, with the nucleus containing one or two large nucleoli and a number of smaller nucleoli.

Early and late-perinuclear oocytes are larger, more ovoid in shape and are less basophilic with a proliferation of nucleoli in the nucleus. The formation of the zona granulosa occurred in late peri-nuclear oocytes. The formation of the zona radiata, a non-cellular membrane formed between the follicular layer (zona granulosa and theca) and the developing oocyte, marking the end of the primary growth phase and was followed by the appearance of primary yolk vesicles (cortical alveoli) in the cytoplasm (Fig. 3.8b).

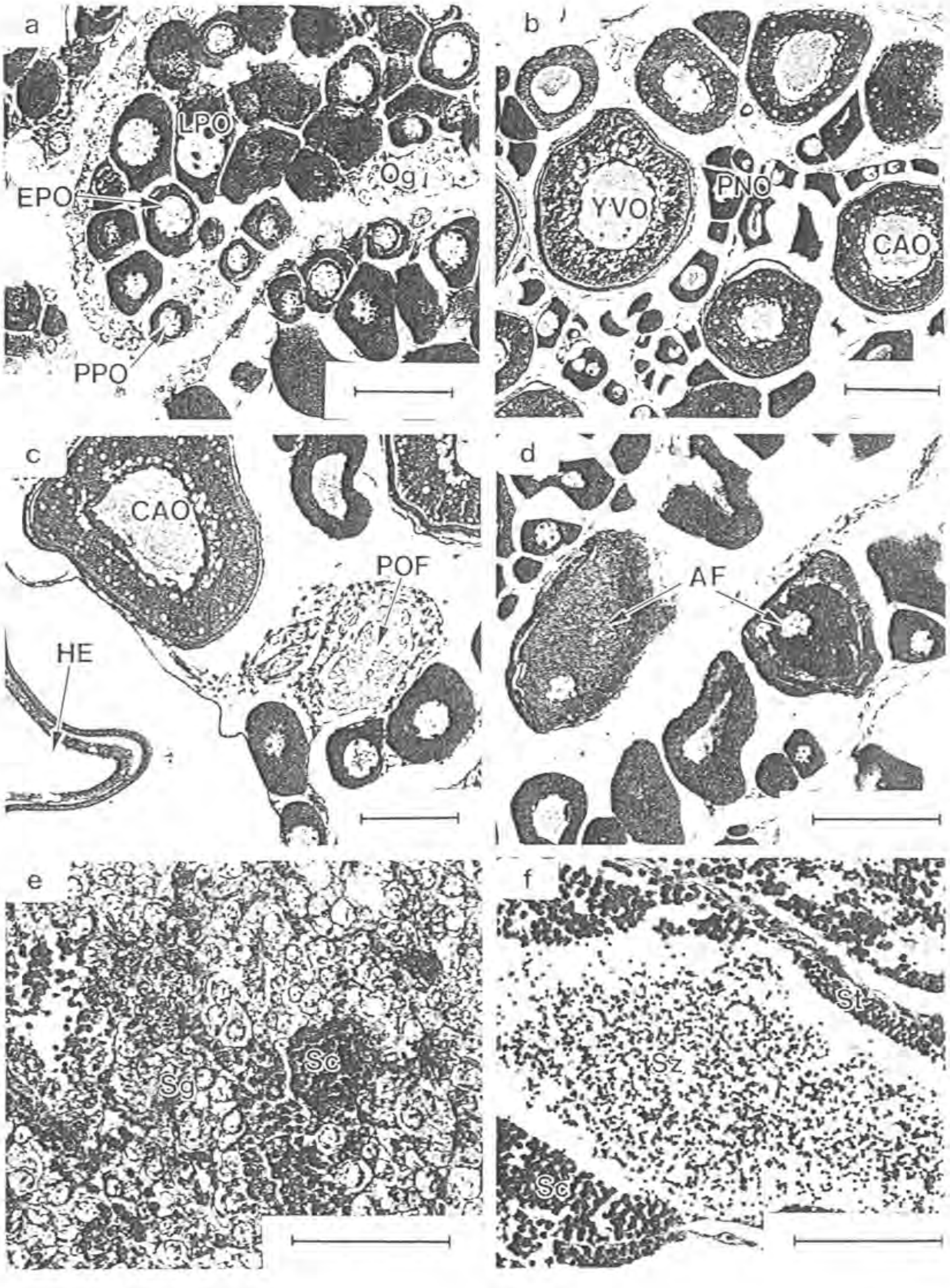

Fig. 3.8. Transverse sections through gonads of *Pterogymnus laniarius* illustrating gametogenesis. (a) Immature ovary containing oogonia (Og), pre (PPO), early (EPO) and late perinuclear oocytes (LPO). (b) The onset of maturation begins with the appearance of primary vesicle oocytes (CAO) with cortical alveoli forming in the periphery of the cytoplasm. Perinuclear oocytes (PNO) and a yolk vesicle oocyte (YVO) are also visible. Secondary yolk vesicle oocytes (YVO) appear with the sequestration of vitellogenic yolk. (C) Hydrated oocytes (HE) and post-ovulatory follicles (POF) were noticeable in the ovaries of spawning fish. (d) Zoning of the cytoplasm was clearly evident in atretic primary vesicle oocytes (AF). (e) Immature testis containing predominantly spermatogonia (Sg) and spermatocytes (Sc). (f) During the breeding season spermatozoa (Sz) fill the lumen. St = spermatids. All scale bars = 200mm. Stained using Gill's haemotoxylin and Papanicoloau's eosin A.

Vitellogenesis was initiated by the appearance of acidophilic 'secondary' yolk globules arising in the region of the cortical alveoli. Later this extravesicular yolk developed throughout the cytoplasm. Yolk accumulation continued until it obscured the cortical alveoli, entirely filling the cytoplasm in the tertiary yolk vesicle stage. During vitellogenesis the nucleus was well-defined with prominent lampbrush chromosomes, chromatin granules and peripheral nucleoli. The cortical alveoli surrounding the nucleus became enlarged, the zona radiata and zona granulosa increased in thickness and the zona radiata became striated. Towards the end of development, the nuclear membrane degenerated, yolk coalesced and a lipid drop formed displacing the nucleus to the oocyte periphery. Histological examination of mature eggs was unsatisfactory with oocytes collapsing during tissue dehydration (Fig. 3.8c). With the ovulation of mature eggs, post-ovulatory follicles remained and these were only visible microscopically in mature ovaries, providing indirect evidence for spawning (Fig. 3.8c). Atresia associated with the termination of gonadal recrudescence was rare and most commonly occurred with ovarian regression during sexual differentiation (Figure 3.8d).

The testes are paired structures, triangular in cross section, surrounded by a tunica albuginea of connective tissue and collagen fibres. They contain a number of seminiferous tubules leading into secondary sperm ducts which join posteriorly to form a main sperm duct.

Spermatogenesis occurs within the seminiferous tubules and is initiated by the mitotic division of the lining spermatogonia which are characterised by their large size, prominent cytoplasm and lightly basophilic nuclear chromatin (Fig. 3.8e). These later gave rise to primary spermatocytes with smaller nuclei. The first meiotic division produced secondary spermatocytes displacing the more advanced spermatocyte stages towards the lumen of the tubule. With the rupturing of the secondary spermatocyte cysts, spermatids were released into the tubule lumen to mature into spermatozoa. Spermatoza, characterised by their small size and intensely basophilic heads, accumulated in the tubules and moved towards and accumulated in the sperm ducts (Fig. 3.8f).

Both oogenesis and spermatogenesis occurred throughout the year with small numbers of hydrated eggs present in almost all mature ovaries sampled. There was no evidence of mass ovarian atresia or flaccid spent ovaries, common in seasonally spawning sparids (Buxton, 1990). All stages of vitellogenesis were present in the ovaries of ripe females suggesting asynchronous, iteropary in the species. The periodicity between spawnings remains unknown. The eggs have a small mature cell size (>500 μm), large oil droplet and are probably pelagic (Buxton 1990). No ripe-running female fish were sampled.

Median female sexual maturity occurred at 204 mm FL (4 years) and total female maturity at 260 mm FL (7 years) (Fig. 3.9). Sex ratios of adult panga (>200 mm FL) were female biased, differing significantly from unity using both research (1 male : 1.7 females; $\chi^2 = 65.3$; $df = 16$; $n = 1322$; $p < 0.05$) and commercial trawling data (1 male : 1.9 females; $\chi^2 = 80.8$; $df = 16$; $n = 1043$; $p < 0.05$). Individual gonadosomatic indices showed that reproductive activity extended throughout the year with activity peaking during the winter months (Fig. 3.10).

*Diet*

Stomach content analysis showed that the panga was an opportunistic benthic predator, feeding on a wide variety of benthic associated prey organisms. Juvenile (<130 mm FL), subadult (130-200 mm FL) and adult fish (>200 mm FL) had distinct feeding patterns which are summarised in Tables 3.7 to 3.9. Overall, crustaceans were the most frequently eaten prey and contributed the greatest volume in all size classes sampled.

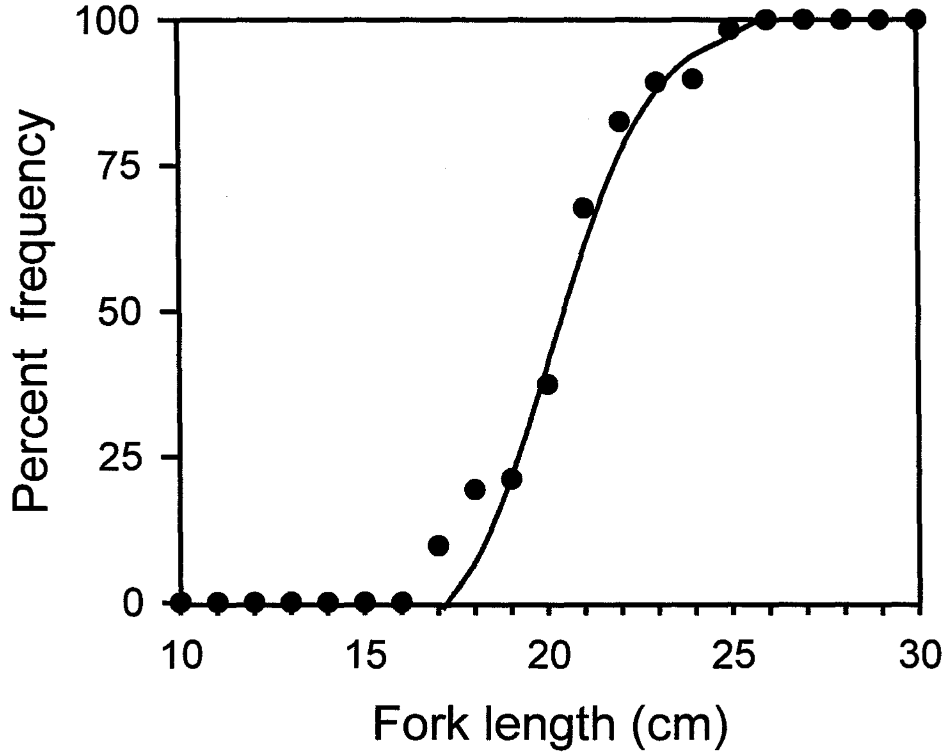

Fig. 3.9. Percent frequency of mature female *Pterogymnus laniarius* in different length classes sampled on the Agulhas Bank between February 1994 and July 1995. The curve was fitted using a logistic ogive.

Juvenile fish fed predominantly in the water column with 86.9% of all the stomachs sampled and 74.9% of all prey eaten being mysids[1], of which the orange-eye mysid was the most important (Table 3.7). Amphipods, despite being present in the diet, were less important both in frequency (36.9%) and in volume (6.2%). Subadult fish showed a shift in feeding habit, moving to the substratum to feed. Ophiuroids were the prefered prey item of subadult fish (42.9%) and volumetrically contributed most (36.8%) to the diet (Table 3.8).

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[1] The taxonomy of mysids is under revision. Voucher specimens have been lodged with the University of Port Elizabeth

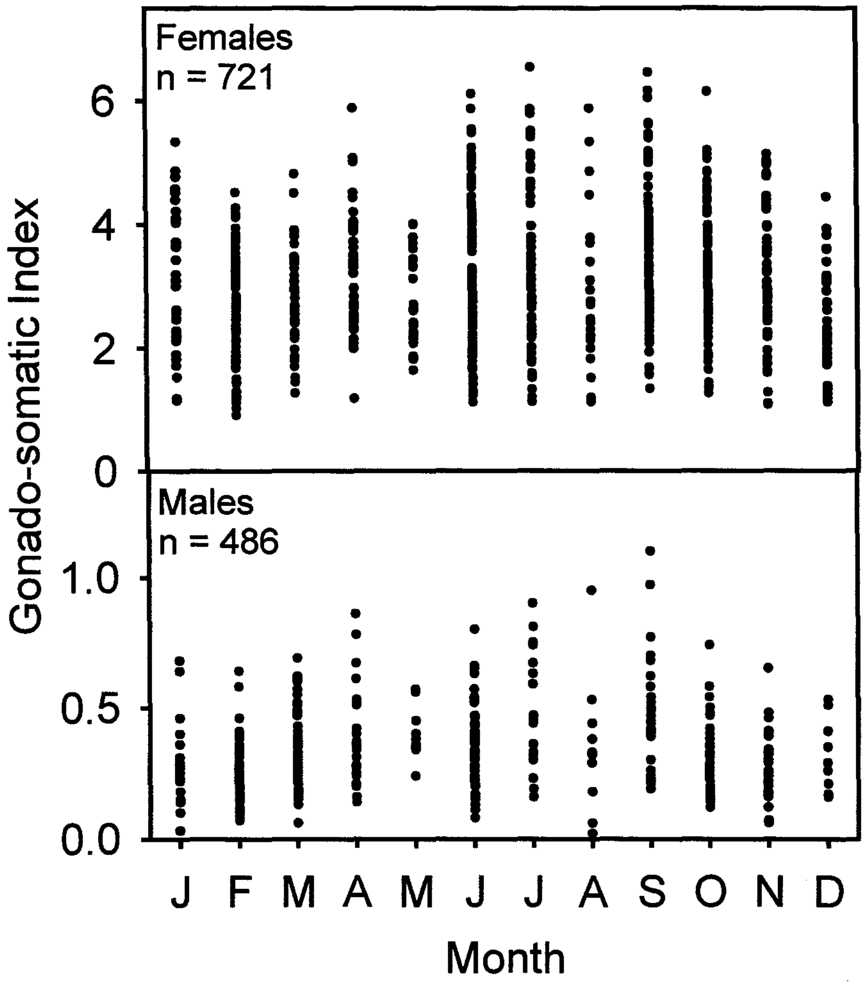

Fig. 3.10. Seasonal variation of individual gonadosomatic indices for male and female *Pterogymnus laniarius* sampled on the Agulhas Bank between February 1994 and July 1995.

Amphipods and mysids were also frequently eaten (59.5% and 30.9%), yet were less important volumetrically (12.2% and 10.3% respectively) and a few brachyurans, macrurans and fish were consumed. Total mortality estimates from the commercial line and trawlfisheries were slightly lower than those obtained from the research trawl data and probably reflect bias in sampling with research trawls selecting fish from a wider size range and sampled over a larger area. Overall, all the estimates were similar, suggesting that this species constitutes one stock on the Agulhas Bank.

Adult fish were almost exclusively benthic feeders, feeding predominantly on soft substrate prey such as the brachyurans, *Gonoplax angulata* and *Mursia cristimanus* . *Gonoplax angulata* was the most commonly eaten prey species (43.0%) and volumetrically contributed to the bulk of the diet (34.2%). Other epibenthic prey such as gammarid amphipods and errant polychaetes, despite being common in the diet (29.1% and 27.5% ), contributed little volumetrically (5.4% and 7.6%). There was evidence of occasional feeding within the water column on the stomatopod, *Pterygosquilla capensis* and the teleost, *Engraulis capensis*.

## Discussion

The modelled length-at-age estimates showed that the panga is a slow growing, long-lived species with a lifespan in excess of 16 years, typical of the Sparidae (Buxton, 1993). Previous studies using scales and unsectioned otoliths recorded ages up to 13 years which resulted in faster predicted growth rates, larger mean lengths-at-age and larger theoretical asymptotic lengths. This appears to be a common trend in studies using scales and unsectioned otoliths for long lived species (Withell and Wankowski, 1988; Milton et al., 1995).

The maximum known length of panga (±400 mm FL; Smith and Heemstra, 1986) was similar to the largest fish obtained in the samples (405mm FL) and successfully aged (394mm FL) in this study. The predicted maximum theoretical length was slightly lower at 380mm FL. The natural mortality estimate of 0.28 year$^{-1}$ was greater than Sato's (1980) estimate of 0.2 year$^{-1}$, whilst also being at the upper end of the range for other temperate sparid species studied which ranged between 0.12 and 0.33 year$^{-1}$ (Pulfrich and Griffiths, 1988a; Buxton, 1992; Vaughan et al., 1992; Punt et al., 1993).

Table 3.7
Stomach content analysis of juvenile *Pterogymnus laniarius* (87-120mm FL), sampled on the Agulhas Bank between February 1994 and July 1995.
(*n* = 46; Rank = %Frequency of occurrence × % visual volume).

| Species | % Frequency of occurrence | % Visual volume | Rank | % Mass |
|---|---|---|---|---|
| **Crustacea** | **100** | **90.49** | **9049** | **78.7** |
| Amphipoda | 36.9 | 6.2 | 229 | 9.6 |
| Aeginellidae | <1 | <1 | <1 | |
| *Ampelisca fusca* | 2.2 | <1 | <1 | |
| *Aora anormala* | 6.5 | <1 | 2 | |
| Coropiidae | 4.3 | <1 | <1 | |
| *Leucolthoe ?richardi* | 4.3 | <1 | <1 | |
| Lysianassidae | 4.3 | 1.9 | 8 | |
| Gammaridae | 11.0 | 1.2 | 13 | |
| *Gammaropsis afra* | 13 | 0.9 | 12 | |
| *Maera bruzeli* | 8.7 | <1 | 7 | |
| *Maera vagans* | <1 | <1 | <1 | |
| *Photis uncinata* | 2.2 | <1 | <1 | |
| Anomura | 4.3 | <1 | 2 | <1 |
| Paguridae | 4.3 | <1 | 2 | |
| *Upogebia capensis* | 2.2 | 2.1 | 4 | |
| Brachyura | 6.5 | 3.2 | 21 | 19.3 |
| Remains | 6.5 | 3.2 | 21 | |
| Copepoda | 15.2 | <1 | 9 | <1 |
| Isopoda | 4.3 | <1 | <1 | 1.8 |
| Macrura | 8.7 | 6.9 | 60 | 2.8 |
| Remains | 8.7 | 6.9 | 60 | |
| Mysidacea | 86.9 | 74.9 | 6509 | 54.7 |
| Orange eye mysid[1] | 26.1 | 23.5 | 613 | |
| Red eye mysid[1] | 63.0 | 3.8 | 239 | |
| Black eye mysid[1] | 2.2 | <1 | 2 | |
| Tanaidacea | 2.2 | <1 | <1 | <1 |
| **Cnidaria** | **2.2** | **<1** | **<1** | **1.4** |
| **Echinodermata** | **4.3** | **1.9** | **8** | **4.4** |
| Ophioroidea | 4.3 | 1.9 | 8 | 4.4 |
| *Amphiura simonsi* | 2.2 | <1 | 2 | |
| Remains | 2.2 | 1.4 | 3 | |
| **Polychaeta errantia** | **8.7** | **1.4** | **12** | **<1** |
| **Pisces** | **4.4** | **2.0** | **9** | **13.3** |
| *Paracallionymus costatus* | 4.4 | <1 | 2 | |
| Remains | 2.2 | <1 | <1 | |
| **Unidentified material** | **2.2** | **1.3** | **3** | **1.4** |
| **Amorphous material** | **2.2** | **<1** | **1** | **<1** |

[1] The taxonomy of mysids is under revision. Voucher specimens have been lodged with the University of Port Elizabeth

Table 3.8
Stomach content analysis of subadult *Pterogymnus laniarius* (130-200 mm FL), sampled on the Agulhas Bank between February 1994 and July 1995.
($n = 42$; Rank = % Frequency of occurrence × % visual volume)

| Species | % Frequency of occurrence | % visual volume | Rank | %Mass |
|---|---|---|---|---|
| **Crustacea** | **69.0** | **41.5** | **2864** | **28.9** |
| Amphipoda | 59.5 | 12.2 | 727 | 3.3 |
| Aeginellidae | 11.9 | 1.2 | 14 | |
| *Ampelisca fusca* | 2.4 | 1.7 | 4 | |
| *Aora anormala* | 4.8 | <1 | <1 | |
| Coropiidae | 2.4 | <1 | <1 | |
| *Ischyrocerus anguipes* | 2.4 | <1 | <1 | |
| *Liljeborgia epistomata* | 2.4 | <1 | <1 | |
| Gammaridae | 31 | 3.9 | 121 | |
| *Gammaropsis afra* | 7.1 | 2.8 | 20 | |
| *Maera bruzeli* | 2.4 | <1 | <1 | |
| *Maera vagans* | <1 | <1 | <1 | |
| *Photis uncinata* | 4.8 | <1 | <1 | |
| *Phtisca marina* | 2.3 | <1 | <1 | |
| *Stenothoe sp.* | 2.4 | <1 | <1 | |
| Anomura | 4.4 | 2.4 | 10.5 | <1 |
| Paguridae | 2.4 | 2.4 | 5.7 | |
| *Upogebia capensis* | 2.4 | <1 | 1 | |
| Brachyura | 11.9 | 9.6 | 114 | 19.3 |
| *Gonoplax angulata* | 4.8 | 3.3 | 16 | |
| *Mursia cristimanus* | 2.4 | 2.4 | 6 | |
| Remains | 7.1 | 3.9 | 28 | |
| Cumacea | 2.4 | <1 | <1 | <1 |
| Macrura | 14.3 | 7.0 | 100 | 4.3 |
| Remains | 14.3 | 7.0 | 100 | |
| Mysidacea | 30.9 | 10.3 | 319 | 1.5 |
| Red eye mysid[1] | 7.14 | 3.8 | 27 | |
| Black eye mysid[1] | 7.14 | <1 | 2 | |
| Remains | 16.7 | 6.2 | 104 | |
| **Echinodermata** | **42.9** | **36.8** | **1579** | **37.3** |
| Ophioroidea | 42.9 | 36.8 | 1579 | 37.3 |
| *Amphipholis strata* | 2.3 | 1.2 | 3 | |
| Remains | 40.5 | 35.6 | 1442 | |
| **Mollusca** | **7.1** | **2.6** | **18** | **7.1** |
| Cephalopoda | 7.1 | 2.6 | 18 | 7.1 |
| *Loligo v. renauldii* | 4.8 | 2.6 | 18.5 | |
| *Sepia* sp. | 2.4 | <1 | <1 | |
| **Polychaeta errantia** | **19.0** | **10.1** | **192** | **9.4** |
| **Pisces** | **7.1** | **6.8** | **49** | **16.5** |
| *Engraulis capensis* | 2.4 | 2.4 | 6 | |
| *Paracallionymus costatus* | 2.4 | 2.3 | 5 | |
| Remains | 2.4 | 2.2 | 5 | |
| **Unidentified material** | **7.1** | **1.8** | **13** | **<1** |

[1] The taxonomy of mysids is under revision. Voucher specimens have been lodged with the University of Port Elizabeth

Table 3.9
Stomach content analysis of adult *Pterogymnus laniarius* (210-394 mm FL), sampled on the Agulhas Bank between February 1994 and July 1995.
(n = 302; Rank = %Frequency of occurrence × % visual volume)

| Species | % Frequency of occurrence | % Visual volume | Rank | %Mass |
|---|---|---|---|---|
| **Crustacea** | **86.1** | **63.1** | **5433** | **73.1** |
| Amphipoda | 29.1 | 5.4 | 158 | 2.3 |
| Aeginellidae | <1 | <1 | <1 | |
| *Ampelisca fusca* | 1.3 | <1 | <1 | |
| *Aora anormala* | 1.7 | <1 | <1 | |
| *Chevalia ariculae* | <1 | <1 | <1 | |
| Coropiidae | <1 | <1 | <1 | |
| *Eripisella capensis* | <1 | <1 | <1 | |
| *Ischyrocerus anguipes* | <1 | <1 | <1 | |
| *Liljeborgia palmata* | <1 | <1 | <1 | |
| *Liljeborgia epistomata* | <1 | <1 | <1 | |
| Lysianassidae | 3.9 | <1 | 4 | |
| *Lysianassa ceratina* | <1 | <1 | <1 | |
| Gammaridae | 14.0 | 2.0 | 28 | |
| *Gammaropsis afra* | 2.6 | <1 | <1 | |
| *Maera bruzeli* | 3 | <1 | 2 | |
| *Maera vagans* | <1 | <1 | <1 | |
| *Paramaera capensis* | <1 | <1 | <1 | |
| *Photis uncinata* | 2.3 | <1 | <1 | |
| *Phtisca marina* | <1 | <1 | <1 | |
| *?Rhachotropis sp* | <1 | <1 | <1 | |
| Anomura | 7.3 | 3.8 | 23 | 5.3 |
| Paguridae | <1 | <1 | <1 | |
| Remains | 1.7 | <1 | 1 | |
| *Upogebia capensis* | 4.3 | 3.4 | 15 | |
| Brachyura | 60.9 | 45.3 | 2757 | 55.8 |
| *Gonoplax angulata* | 43.0 | 34.2 | 1470 | |
| *Macropodia falcifera* | 2.3 | <1 | <1 | |
| Megalopa larvae | <1 | <1 | <1 | |
| *Mursia cristimanus* | 6.4 | 3.3 | 21 | |
| Dromiidae | <1 | <1 | <1 | |
| Remains | 14.9 | 6.9 | 102 | |
| Cumacea | <1 | <1 | <1 | <1 |
| Isopoda | 1 | <1 | <1 | <1 |
| Macrura | 7.6 | 2.2 | 17 | <1 |
| *Chlorotocus crassicornis* | <1 | <1 | <1 | |
| *Gennadas sp.* | <1 | <1 | <1 | |
| *Rhynchocinites durbanensis* | <1 | <1 | <1 | |
| Remains | 6.3 | 2.0 | 13 | |
| Mysidacea | 18.2 | 1.5 | 27 | <1 |
| Orange eye mysid[1] | 1.3 | <1 | <1 | |
| Red eye mysid[1] | 1.9 | <1 | <1 | |
| Black eye mysid[1] | 12.6 | 1.1 | 14 | |
| Remains | 2.9 | <1 | <1 | |
| Ostracoda | <1 | <1 | <1 | <1 |
| Stomatopoda | 5.3 | 4.0 | 21 | 9.9 |
| *Pterygosquilla a. capensis* | 5.3 | 4.0 | 21 | |
| Remains | <1 | <1 | <1 | |
| Tanaidacea | 1 | <1 | <1 | <1 |
| **Bryozoa** | **<1** | **<1** | **<1** | **<1** |
| **Cnidaria** | **6.6** | **1.5** | **10** | **1.2** |
| **Echinodermata** | **19.2** | **8.3** | **160** | 110.0 |
| Asteriodea | <1 | <1 | <1 | 0.01 |
| Echinodea | <1 | <1 | <1 | 0.01 |

| | | | | |
|---|---|---|---|---|
| Ophioroidea | 18.0 | 8.0 | 144 | 13.4 |
| *Amphipholis strata* | <1 | <1 | <1 | |
| *Amphiura atlantica* | 1.7 | <1 | <1 | |
| *Amphiura simonsi* | 3.9 | 1.1 | 4 | |
| *Ophiothamnus remotus* | 2 | 1 | 2 | |
| *Ophithrix fragalis* | <1 | <1 | <1 | |
| Remains | 11.9 | 4.9 | 58 | |
| **Mollusca** | **11.26** | **3.4** | **39** | **2.4** |
| Cephalopoda | <1 | <1 | <1 | |
| *Loligo v. renauldii* | <1 | <1 | <1 | |
| *Sepia sp.* | <1 | <1 | <1 | |
| Gastropoda | 5.0 | 1.3 | 7 | |
| *Atys sp* | <1 | <1 | <1 | |
| *Cingula ?argentea* | <1 | <1 | <1 | |
| *Nassarius quantulus* | <1 | <1 | <1 | |
| *Neograstropoda remains* | <1 | <1 | <1 | |
| *Ilanga laevissima* | <1 | <1 | <1 | |
| *Philine cf. subquadrata* | <1 | <1 | <1 | |
| *Pleurobranchia* sp. | <1 | <1 | <1 | |
| Remains | 2 | <1 | 1 | |
| Pelecopoda | 5.6 | 2.2 | 12 | |
| *Abra ?alfredensis* | <1 | <1 | <1 | |
| *Chlamys sp.* | 2 | <1 | <1 | |
| *Limaria sp.* | <1 | <1 | <1 | |
| *Macoma crawfordi* | 1.0 | 1.0 | 1 | |
| *Pododesmus ?rufanensis* | <1 | <1 | <1 | |
| *Pitar sp.* | <1 | <1 | <1 | |
| Remains | 2 | <1 | 1 | |
| Scaphopoda | <1 | <1 | <1 | <1 |
| **Nemertea** | **1.7** | **<1** | **<1** | **<1** |
| **Polychaeta errantia** | **27.5** | **7.6** | **209** | **5.1** |
| **Pisces** | **19.2** | **10.3** | **198** | **17.9** |
| *Champsodon capensis* | <1 | <1 | <1 | |
| *Cynoglossus zanzibarensis* | <1 | <1 | <1 | |
| *Diplogaster megalops* | <1 | <1 | <1 | |
| *Engraulis capensis* | 4.6 | 3.0 | 14 | |
| *Sardinops sagax* | <1 | <1 | <1 | |
| *Paracallionymus costatus* | 4.0 | 1.4 | 6 | |
| *Lepidopus caudatus* | <1 | <1 | <1 | |
| Scales | 2.9 | <1 | <1 | |
| Remains | 29.9 | 5.2 | 52 | |
| **Unidentified material** | **6.6** | **1.9** | **13** | **<1** |
| **Amorphous material** | **8.6** | **1.7** | **15** | **1.1** |

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[1] The taxonomy of mysids is under revision. Voucher specimens have been lodged with the University of Port Elizabeth

The difference between macroscopical and histological based descriptions of gonadal ontogeny stresses the need for a histological approach if an accurate description is to be achieved. This explains why various authors such as Hecht and Baird (1977) and Uozumi et al. (1981; 1985) described this species as a protogynous hermaphrodite based on the presence of males in the larger size classes preceded by visibly intersexual individuals and a female biased sex ratio. The microscopic examination of the gonads showed that the panga are late gonochorists with functional ovaries and testes developing from an immature intersexual ovotestis. Late gonochorism has been found to be a common reproductive style amongst sparids (Coetzee, 1983; 1986; Francis and Pankhurst, 1988; Matsuyama et al., 1988; Smale, 1988; Buxton and Garratt, 1990) with less dramatic management implications than sex changing species. In sex changing species, in which fishing effort is directed towards large individuals can lead to a reduction in any one sex, altering the sex ratio within the population and possibly impairing spawning behaviour (Buxton, 1992).

The relative size of the ovary and testis was interesting because it more closely approximated sex changing, rather than late gonochoristic, sparids (Buxton and Garratt, 1990). Broadcast pair spawners tend to have smaller testes, while large testes are indicative of group spawning (Choat and Robertson, 1975) and are selected under conditions of intense sperm competition. Sexual dimorphism in gonad size is not the norm in late gonochoristic sparids. Further evidence of a female biased sex ratio suggests that the panga may have a spawning style similar to sex changing rather than other late gonochoristic species in which sex ratio and ovary/testes size are similar.

Unlike most other sparids which have a seasonal breeding period, the panga spawns throughout the year over the Agulhas Bank. This confirms Budnichenko and Dimitrova's (1970), Sato's (1977) and Uozumi et al.'s (1981; 1985) preliminary observations, but contradicts Hecht and Baird (1977) who proposed a breeding period between mid-September to May, founded predominantly on macroscopic staging even though their reported gonadosomatic indices showed trends similar to those found in this study. Other evidence for reduced seasonal spawning in sparids has been reported for *Pachymetopon blochii*, a South African west coast species, by both Nepgen (1977) and Pulfrich and Griffiths (1988a). Both studies showed that spawning activity occurred throughout the year, peaking during the spring and autumn equinox. Other sympatric Agulhas Bank species either have a discrete spawning season such as *Genypterus capensis* (Japp, 1989) or more commonly, a protracted spawning season with one or more peaks in reproductive activity as in *Merluccius capensis*, *Austroglossus pectoralis* (Payne, 1986), *Chelidonichthys capensis* (Hecht, 1976; Wood-McPhail, in prep.), *Chelidonichthyes queketti* (Booth, in press) and *Cynoglossus zanzibarensis* (Booth and Walmsley, in prep.).

The endemism of many sparid species prevents the comparison of seasonal and non-seasonal spawning patterns in populations inhabiting different oceanographic conditions. Non-seasonal spawning with an increase in activity over spring and autumn was found, however, to be common in many insular lutjanid populations inhabiting areas with low amplitude oceanographic cycles (Grimes, 1987). In his review of lutjanid reproduction, Grimes (1987) showed that spawning seasonality appeared to be correlated to production and food availability. If production is low and continuous and food is scarce and patchy, then spawning will be continuous and in small batches, a 'bet hedge' against starvation and predation. There appears to be reduced seasonality on the Agulhas Bank, with little temperature fluctuation (range = 9-15°C; mean = 12°C) and little wind-driven upwelling resulting from the warm, non-seasonal Agulhas Current. Coastal, wind-driven upwelling has been attributed to causing heavy larval mortalities in seasonally spawning, littoral sparid species (Tilney and Buxton, 1994).

Dietary differences between the dietary studies confirm the panga is an opportunistic benthic predator. It exhibits a clear ontogenetic shift in feeding habits, moving from the water column to the benthos to feed. Juveniles feed predominantly on mysids in the water column. This shift corresponds with a change in dentition. The developing molariform teeth enable subadult fish to feed on larger, harder prey such as ophiuroids and brachyurans. A double row of molariform teeth were well developed in adult fish and together with their characteristic flaring canines enable them to feed on a wide variety of prey items. Hard shelled prey such as crabs and ophiuroids are preferred as these are easily crushed. Prey were dominated by soft substratum associated organisms suggesting that the panga feeds on sand and mud depressions between rocky outcrops and low profile reef. Hecht (1976) and Clarke and Buxton (1985) also recorded a high predominance of prey species associated with soft substrates and suggested that the panga's villose lips, which are similar to those found in *Lithognathus lithognatus*, are possibly tactile and sensory and well suited to a soft substrate feeding lifestyle. Similar dietary trends were found in both *Calamus leucostegus* and *Pagrus pagrus*. Both species prefer reef areas and move onto soft substrata to feed where they also exhibited an ontogentic shift in diet with the corresponding change in dentition, enabling the adults to feed on brachyurans and molluscs (Manooch, 1977; Sedberry, 1989).

Despite the fact that panga is presently the most heavily exploited sparid species in South African waters, it is one of a few South African sparid species showing possible potential for further exploitation. Generally, several life history characteristics make sparid fishes poor candidates for exploitation. In contrast, several biological characteristics may possibly contribute to the panga's resilience as an exploitable species. Its late gonochoristic reproductive style has been shown to reduce the impact of fishing effort on larger size groups whilst a protracted spawning season alleviates the need for a closed season. Although selection occurs after sexual maturity in this species (a consequence of both a minimum stretched mesh size of 75mm and the undesirability of small fish in the market), this needs to be closely monitored as fish were selected by the directed foreign fishery in the early 1960's and 1970's at an age of 2.5 years, 1.5 years before sexual maturity. This almost certainly contributed to the rapid decline in the stock. Hopefully, the present conditions within the fisheries harvesting this species will continue to provide a mechanism for maintaining recruitment at its present level. The panga's preference for soft substratum prey and its wide diet enables it to exploit large areas of the Agulhas Bank such as low/high profile reef and mud-reef/sand-reef interfaces, contributing to it's large biomass in contrast to other sparids in the region. The longevity, slow growth and low natural mortality rate of this species is of concern, mitigating against the above factors. These make the stock more prone to over-exploitation due to a rapid reduction in surplus production. It is for this reason that fishing effort will need to be carefully monitored as the response of a long lived, slow growing species to increasing fishing levels is slow and difficult to detect, often having disastrous management consequences. Given the low estimates of fishing mortality and the reduced fishing pressure over the past two decades (Chapter 1), it appears that the panga stock is either under- or at most fully exploited. It is, therefore, necessary that an age-structured stock assessment approach is applied to the stock using the parameter estimates derived from this chapter to assist in the development of a strategy for the sustainable utilisation of this species on the Agulhas Bank.

# Chapter 4 - Understanding the distribution and abundance of panga using a Geographical Information System approach

## Introduction

Data collected from field surveys be they biological, geological or socio-economic have a spatial component. This is most often ignored or only given minor consideration if these data, in particular abundance estimates, form the basis of many forms of fisheries assessments *inter alia* VPA (Pope and Shepherd, 1985; Punt, 1994), age structured production modelling (Punt and Japp, 1994; Punt et al., 1995) and integrated analysis (Deriso et al., 1985). If the spatial aspect of fish abundance is ignored, particularly in commercial *CPUE* data or fishery independent biomass survey estimates, it may lead to unreliable abundance indices.

Spatial analysis of demersal fish communities in South Africa has been confined in the past to estimating mean or total abundance with their associated variances on a temporal scale (Badenhorst and Smale, 1991). These indices are most often based on the standard estimators for random stratified sampling designs (Mackett, 1973) with depth as the major stratifying variable (Smith 1990, Smale and Badenhorst, 1991). These temporal trends in fish abundance can now be incorporated into stock assessment models or most models can be modified for them to be incorporated later (Fournier and Archibald, 1982; Deriso et al., 1985; Gavaris, 1988; Punt and Japp, 1994; Punt et al., 1995).

Various statistical methods have been developed to interpret and incorporate spatial trends in various forms of analyses. For the purposes of this study a spatial trend is defined as the change in the average value of a response variable such as abundance which is a function of its spatial location (Kaluzny, 1987). Spatial analysis deals with data that is geo-referenced, in that it has a spatial component. As survey data are geo-referenced with respect to longitude and latitude they are ideal candidates for this form of analysis. Apart from the geo-referenced nature of the data, survey data are also multivariate in that each trawl will often have counts of the numbers of individuals from various species, simultaneous collection of physical and other pertinent biological data.

Fisheries biomass surveys can also allow for the spatial analysis of distribution patterns of marine populations and how they might be related to physical (depth, temperature, dissolved oxygen levels, sediment type) or biological (co-distribution with other species or proximity to spawning or feeding grounds) parameters. Methods to detect and correct for these trends could, therefore, lead to improved abundance estimates (Swartzman et al., 1992).

An increasing trend in spatial analysis has been from a geostatistical perspective (Journel and Huijbregts, 1978; Sullivan, 1991). These models analyse spatial autocorrelation, where the correlation between variables over space is considered to be a function of the distance between them. This forms the theory behind the construction of semi-variograms to understand the spatial structure of the data and then to incorporate these trends into a prediction of abundance using kriging. As kriging predictions are sensitive to the modeled variogram, variographic analysis is central to the estimation process. Alternatively, another method used to analysis spatial trends is the use of Generalized Models (Nelder and Wedderburn, 1972; McCullagh and Nelder, 1989; Hastie and Tibshirani, 1986; 1990). Here, the response variable (density or count data) can be modeled as a function of two (latitude, longitude) or more (physical, biological or geological) covariates.

An approach that incorporates various qualitative and statistically robust methods to interpret this geo-referenced and multivariate data is the use of a Geographical Information System (GIS). An information system is a chain of operations that takes place from planning the observation and collection of data, to the use of the derived information in some decision-making process. Using this definition, a GIS is an information system that is specifically designed to work with data referenced by spatial or geographic co-ordinates. In other words, a GIS is both a database system with specific capabilities for spatially-referenced data, as well as a platform for analytical operations for working with the data (Star and Estes, 1990). In addition, the strength of a GIS is that it can integrate disparate data types which are geo-referenced with a highly graphical user interface. It can allow for the analysis of both qualitative and quantitative data types, identify associations between components and therefore build a "living database" with exploratory data analysis, as well as interpretative and mapping capabilities.

The panga, was chosen as a candidate species to illustrate the development and application of a marine fish GIS. Whilst aspects of its general biology are relatively well known (Chapter 3), little is known about the spatial distribution and abundance dynamics of this species apart from the general descriptive work by Uozumi et al. (1981; 1985), Hatanaka et al. (1983), Badenhorst and Smale (1991) and Smale et al. (1993) This study comes at a time when there is increased pressure from the commercial fishing sector to develop a directed fishery for this species. There is a clear need for a better understanding of the spatial dynamics of this species in relation to the physical environment in which it occurs. These trends can highlight nursery areas, areas of high spawner biomass, elucidate migratory patterns and to estimate biomass.

## Materials and methods

### *Biomass surveys*

Biomass survey data used in the analysis was collected during biannual biomass assessment surveys on the *F.R.S. Africana* between 1988 and 1995 (Fig. 4.1). The sampling methodology used is described in Chapter 2. In addition, physical data, including depth, bottom temperature, salinity and dissolved oxygen, were collected at the end of each trawl using a conductivity, temperature and depth (CTD) rosette sampler to within 10m of the bottom (Table 4.1).

### *Fish life history stages*

A life history stage classification proposed in Chapter 3 was adopted to disaggregate the biomass of the stock and provide results on each stanza in the life history of the species. The classification system adopted, incorporates information on both reproductive and feeding biology. Juvenile fish (< 13 cm TL = 12 cm FL) were characterised by immature gonadal development, feeding predominantly in the water column on mysids. Subadult fish (13 - 23 cm TL = 12 - 21 cm FL) were predominantly immature, with few fish maturing later in the life history stage with size-at-sexual maturity occurring 22 cm TL (= 20 cm FL). Subadult fish exhibited intermediate feeding habits, with components of both the juvenile and adult diets. These fish, preyed on soft prey organisms such as mysids and carid prawns, and as the molariform teeth developed, harder shelled prey such as ophiuroids and brachyurans. Adult fish (>23 cm TL = 22 cm FL) were sexually mature having well developed molariform teeth enabling them to feed on hard shelled brachyuran prey. Fish were grouped by length rather than age as this reduced any inherent ageing bias. This was of concern as ageing was found to be problematic in this species due to the heavily calcified sagittal otoliths (Chapter 3). The suggested life history classification, therefore, incorporates both general life history trends and assumes that at least all fish <13 cm TL were juveniles and that fish >23 cm TL were mature.

*Geographical Information System design*

A simple Windows NT©,[2] based Geographical Information System was developed using ArcView 3.0©,[3]. All statistical analysis was conducted using S-PLUS©,[4] as a high end programmable user interface which can incorporate tab-delimited ASCII text attribute files. The statistical results in the form of summaries and coverages were exported back into ArcView© for further manipulation and graphical presentation. Most figures in this chapter were generated from the developed GIS to illustrate the ease of interpretation and reasonable output quality, thereby reducing the need for additional cartographic assistance. This also stresses the dynamic nature of the GIS as it can easily incorporate new data to the existing database, allow for reanalysis with relative ease with the output being easily generated and interpreted.

Each trawl was treated as a point on the latitude-longitude plane with each biomass survey being converted into a point coverage using decimal degree co-ordinates. The latitude and longitude of the starting of the trawl was used for the points to represent the trawl path vector and the area of the trawl and other attributes such as the CTD and biological data appended as an attribute file. The coastline and bathymetry coverages were digitized from available nautical maps.

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[2] Registered trademark of Microsoft Corporation
[3] Registered trademark of ESRI Inc.
[4] Registered trademark of Mathsoft

The developed GIS was capable of conducting both qualitative and quantitative analyses. Trends in panga distribution and abundance were identified in relation to various physical variables. Both methods are described below.

*Qualitative analysis*

Using overlaying procedures characteristic of most GISs, relationships between covariates can be investigated. Both point and polynomial interpolated physical data (to allow for better visual interpretation) were overlaid with the density of fish.nm$^{-2}$ in each life history stage. Trends were identified using Boolean logic (inequalities applied to sets used to identify *inter alia* unions and intersections) to select alternative combinations of values within the different coverages to identify zones of physical preference.

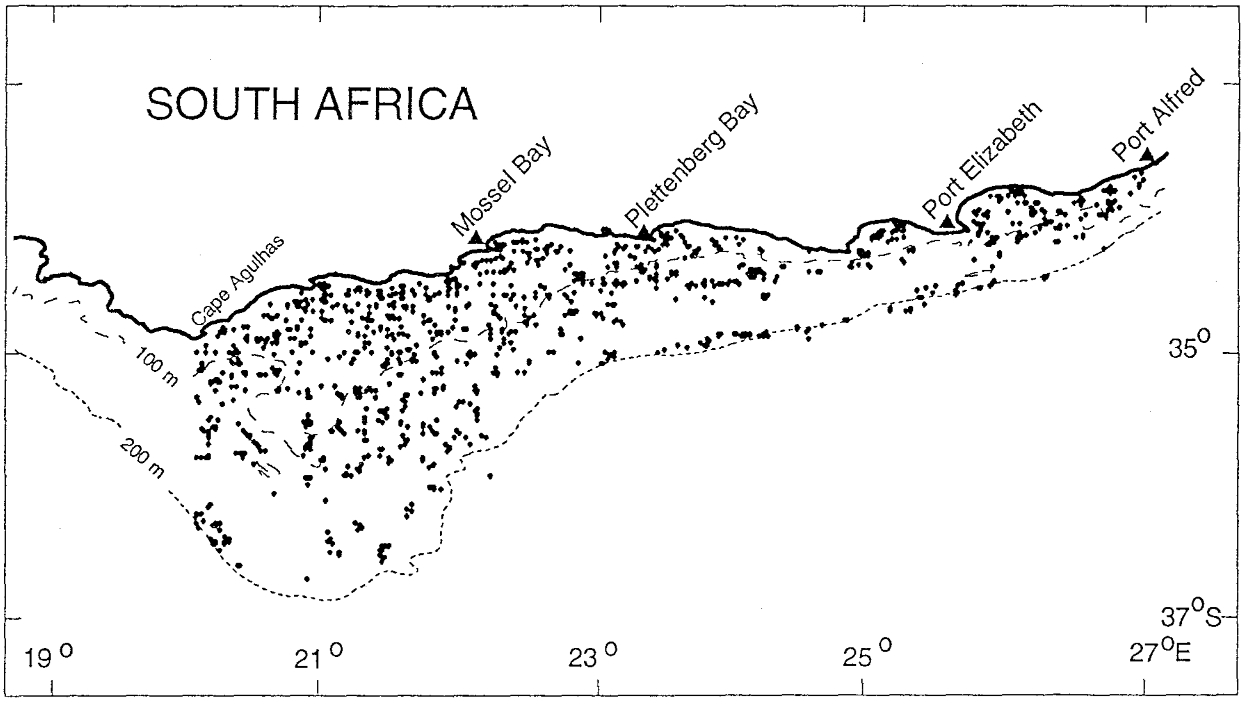

Fig. 4.1. Map illustrating the Agulhas Bank, South Africa with the position of all stations trawled during the period 1988-1995.

*Quantitative analysis*

Two methods were employed. Firstly, fish density was modelled as function of the selected physical and spatial variables within a rigorous statistical framework. Secondly, these trends were incorporated into generating biomass estimates.

Table 4.1
A summary of south coast biomass cruises within South African waters between 20°-27°E. The mean (± standard deviation) and range (in parentheses) of the physical data were sampled using a CTD rosette sampler within 10m of the substratum. Spring / Summer cruises occurred between September and October whilst autumn / winter cruises occurred between April and July.

| Cruise Number | Date | Total trawls | Trawls with *P. laniarius* | Trawls for analysis | Depth (m) | Temperature (°C) | Dissolved Oxygen (mg.l$^{-1}$) |
|---|---|---|---|---|---|---|---|
| SC 063 | May/Jun 1988 | 93 | 67 | 84 | 117.36±79.61<br>(30-450) | 11.13±1.48<br>(9.28-18.47) | 3.83±0.92<br>(1.97-5.53) |
| SC 072 | May 1989 | 62 | 49 | 55 | 100.59±39.02<br>(32-185) | 10.59±1.59<br>(8.8-16.05) | 3.70±0.89<br>(1.85-5.19) |
| SC 082 | May/Jun 1990 | 58 | 54 | 57 | 100.88±58.91<br>(30-480) | 11.85±2.14<br>(9.54-17.17) | 3.64±1.13<br>(1.64-5.42) |
| SC 086 | Sep 1990 | 91 | 47 | 72 | 79.56±43.22<br>(18-224) | 12.44±2.23<br>(8.11-16.21) | 4.47±0.67<br>(3.25-5.91) |
| SC 093 | Jun/Jul 1991 | 91 | 70 | 82 | 109.69±66.41<br>(33-362) | 11.54±2.20<br>(8.13-16.25) | 4.07±0.68<br>(2.47-5.56) |
| SC 095 | Sep/Oct 1991 | 75 | 60 | 68 | 81.64±24.87<br>(31-144) | 13.78±1.69<br>(9.97-17.44) | 4.85±0.70<br>(3.76-5.99) |
| SC 102 | Apr 1992 | 82 | 60 | 44 | 110.17±60.71<br>(30-400) | 11.04±0.78<br>(9.29-13.16) | 3.75±0.78<br>(2.02-4.90) |
| SC106 | Sep 1992 | 87 | 67 | 69 | 80.32±26.64<br>(25-124) | 13.63±2.14<br>(9.33-16.42) | 4.68±0.68<br>(3.36-5.87) |
| SC 111 | Apr/May 1993 | 104 | 89 | 101 | 109.89±43.52<br>(29-237) | 10.53±1.68<br>(7.70-18.16) | 4.05±0.45<br>(2.72-4.79) |
| SC 116 | Sep 1993 | 105 | 85 | 67 | 90.30±30.73<br>(29-186) | 12.58±2.41<br>(8.40-16.30) | 4.53±0.60<br>(3.55-5.98) |
| SC 122 | Jun/Jul 1994 | 88 | 65 | 78 | 123.74±87.02<br>(35-500) | 11.75±2.88<br>(6.59-2.88) | 4.28±0.83<br>(1.36-5.65) |
| SC 125 | Sep/Oct 1994 | 92 | 66 | 66 | 82.93±31.31<br>(30-200) | 12.04±1.57<br>(9.50-15.13) | 4.39±0.83<br>(3.12-9.2) |
| SC 129 | Apr/May 1995 | 95 | 64 | 75 | 138.18±98.09<br>(29-483) | 10.25±1.83<br>(8.30-16.20) | 3.86±0.83<br>(1.80-6.02) |
| SC 131 | Sep/Oct 1995 | 96 | 73 | 81 | 90.51±37.75<br>(28-193) | 12.06±2.24<br>(9.20-16.62) | 4.26±0.65<br>(3.03-6.19) |

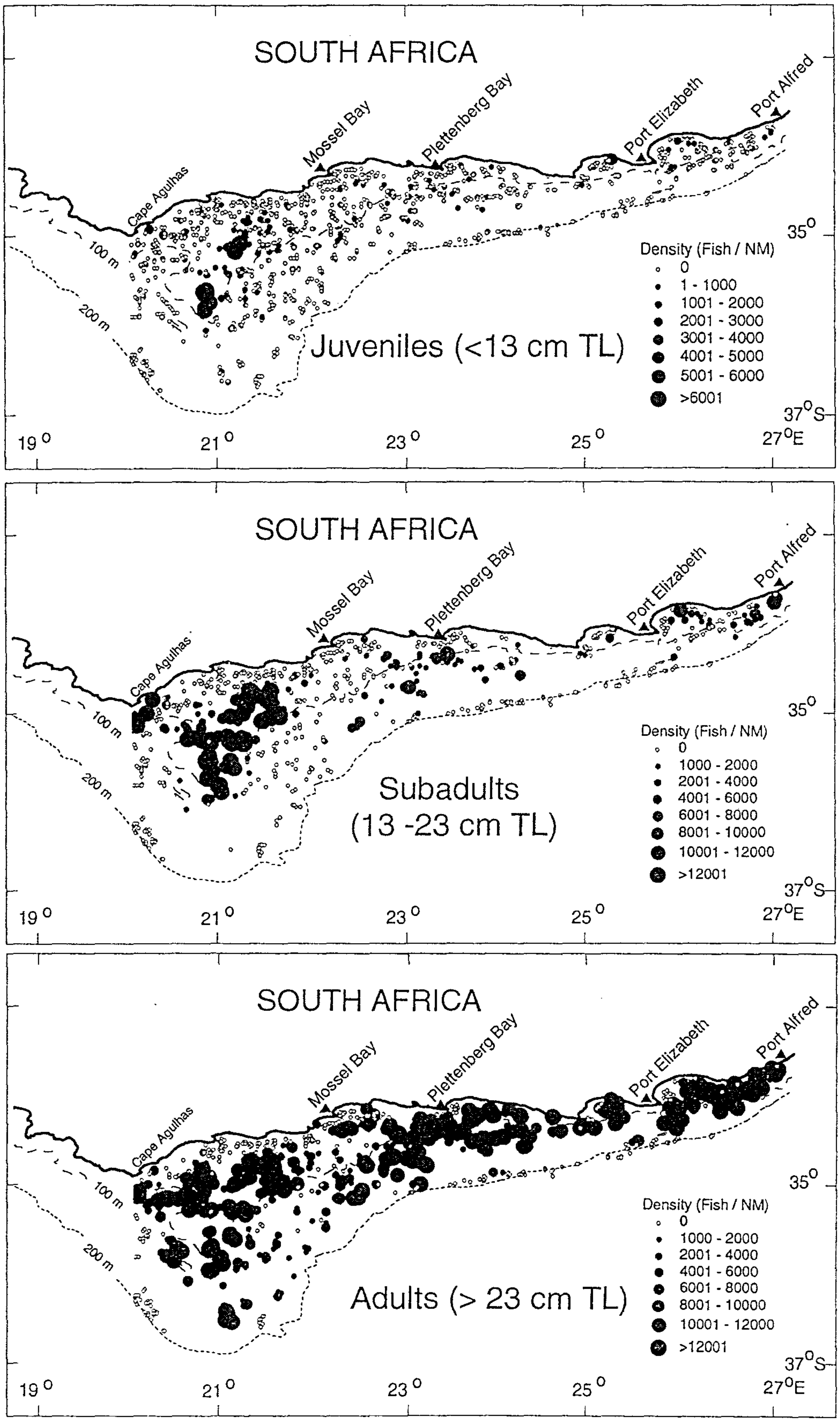

Fig. 4.2. Distribution of three life history stages *Pterogymnus laniarius* on the Agulhas Bank. Data was collected between 1988 and 1995.

Generalized Additive Modelling (GAM) was used to model the spatial distribution and abundance of panga on the Agulhas Bank in response to various predictors (covariates) such as latitude, longitude, temperature, depth and dissolved oxygen. From general observation it was noted that distributions of different life history stages were not homogenous over their distributional range (Fig. 4.2). It was also assumed that the densities of the different life history stages were determined by an underlying Poisson process with the magnitude of the response variable (in this case fish density.$nm^{-2}$), being a function of at least two covariates - latitude and longitude. The use of GAM allows for changes in abundance to be related to spatial covariates without a restriction in the functional form of the relationship (Hastie and Tibshirani, 1990). This method allows for the incorporation of non-linear (and possibly non-parametric) trends into the working model and to include covariates which could potentially determine spatial distribution. The use of GAM to analyse survey data is general in that the response surface that is fitted to the data is only restricted to be a sum of smoothing non-parametric functions. They are similar in form to Generalized Linear Models which use polynomials as functions (Nelder and Wedderburn, 1972). In contrast, GAMs use smoothing functions which allow for the incorporation of local spatial trends while observing these trends over the entire sample space. GAM can, therefore, be considered as a non-parametric generalization of multiple linear regression. Details regarding the use of GAM in this GIS are given as follows.

Generalized Additive Modelling - an overview

Likelihood-based regression models are important and powerful tools in data analysis. Typically, a likelihood is assumed for a response variable $Y$, and the mean of some other parameter. It is modelled as a linear function $\sum_{i=1}^{n} \beta_i X_i$ of a set of covariates $X_1, X_2, \ldots, X_n$. The parameters of the linear function are estimated by maximum likelihood. Normal linear regression and logistic regression are commonly used examples. These models assume a linear form of the covariate effects.

An increasing trend is to move away from linear functions and model the dependence of $Y$ on $X_1, X_2, \ldots, X_n$ in a more non-linear, non-parametric fashion. For a single covariate, such a model would be modelled as $Y = s(X) + \varepsilon$. The error term $\varepsilon$ can have any suitable statistical distribution and s $(X)$, is an unspecified smooth function also known as a scatterplot smoother. This can be extended for $n$ covariates where $\boldsymbol{X} = (X_1, X_2, \ldots, X_n)$. One can, therefore, use a $n$-dimensional scatterplot smoother to estimate s($\boldsymbol{X}$), or assume a less general model such as an additive model s $(\boldsymbol{X}) = \sum_{i=1}^{n} s_i(X_i)$ and estimate it iteratively (Hastie and Tibshirani, 1986). The technique used for estimating s (.)'s, called the local scoring algorithm, uses scatterplot smoothers to generalize the usual Fisher scoring algorithm for computing maximum likelihood estimates (Hastie and Tibshirani, 1990). These smooth functions can be used for data description and prediction.

Generalized additive models are a synthesis of three statistical tools; scatterplot smoothers, additive models and generalized linear models. Whilst Hastie and Tibshirani (1990) give a comprehensive analysis of the various components, those used in this analysis are outlined briefly below.

In an additive model, the expected value of a random variable $X$ is expressed as sum of the smooth functions of the different covariates.

$$\mathrm{E}\,(X|x_i, \ldots, x_n) = \sum_{i=1}^{n} S_i(x_i) \qquad \text{(Equation 4.1)}$$

where $S_I(x_i)$, in this case, represent cubic *B*-spline smoothers of the *n* covariates (Silverman, 1985; Green and Silverman, 1994). A feature of GAM is the incorporation of the exponential family of distributions (Gaussian, Poisson and Binomial). This is particularly suitable for count or density data which follows a Poisson distribution. This is made possible by modelling the sum of the smooth functions as the known function of the expected value of a random variable, the link function. Assuming that the survey data are distributed according to a non-homogenous Poisson distribution, the parameter of the Poisson distribution is calculated as:

$$\Lambda(x) = \int_{Ax} \lambda(u)\, du \qquad \text{(Equation 4.2)}$$

where $\lambda$ $(u)$ is the intensity of the underlying Poisson process and $A_x$ is the area of the observations. The expected value of the Poisson distribution is $\Lambda(x)$ and the link function is the natural logarithm. Thus the Poisson generalized additive model relates the expected counts to the covariates as

$$ln\left[\mathrm{E}(X|x_1,\ldots,x_n)\right] = ln\left[\Lambda(x)\right] = \sum_{i=1}^{n} S_i(x_i) \qquad \text{(Equation 4.3)}$$

Or , if the additive predictor is $\eta = \sum_{i=1}^{n} S_i(x_i)$, then $\Lambda = \mu = e^{\eta}$.

Since the functional form of the smooth functions $S_i(x_i)$ $\forall$ $j = 1,.., n$ is not specified, maximum likelihood estimation techniques cannot be used. An algorithm to maximise the expected log-likelihood is used. The derivative of the expected log-likelihood is set to zero, and resultant equation expanded in a Taylor series about the initial estimate of the additive predictor $\eta^{\circ}$. The equation is then rearranged to give a new estimate of $\eta$ based on the initial estimate of the predictor $\eta^{\circ}$. This update equation is used iteratively with the conditional expectation from the expected log-likelihood estimated by a scatterplot smoother. This algorithm is similar to the adjusted dependent variable regression for computing maximum likelihood estimates when the predictor $\eta$, is a linear function of the covariates (Nelder and Wedderburn, 1979). The adjusted dependent variable for the Poisson generalized additive model at the $m^{\text{th}}$ iteration is

$$z^m = \eta^m + \frac{(y - e^{\eta^m})}{e^{\eta^m}} \qquad \text{(Equation 4.4)}$$

The scatterplot smooth of $z^m$ on $x$ (for this single covariate example) provides an updated estimate of the additive predictor $\eta^{\text{m+1}}$.

The measure of fit for the GAMs is the deviance which is calculated as twice the natural logarithm of the likelihood ratio between the saturated model and the current model. For a Poisson process this can calculated as follows:

$$\text{Deviance}\,(x, \mu) = 2\sum_{\text{i=1}}^{\text{n}} x_{\text{i}} ln\left[\frac{x_i}{\mu_i}\right] - (x_i - \mu_i) \qquad \text{(Equation 4.5)}$$

The updating iterations are continued until the deviance fails to change.

Whilst the above equations contain only one covariate, spatial models consider at least two covariates such as latitude and longitude. Smooth functions were fitted to all covariates considered in the model by the use of a backfitting algorithm. Each successive smooth function for each covariate was fixed and partial residuals estimated. To do this for the $j^{th}$ covariate, $x_j$, the partial residual is calculated as

$$r_j = z - S_0 - \sum_{i \neq j} S_i(x_i) \qquad \text{(Equation 4.6)}$$

where $z$ the adjusted dependent variable described previously, is estimated. An updated value of $S_j$ is computed by smoothing $r_j$ on $x_j$. The process is then repeated for each covariate. The initial estimates for the algorithm are zero for the smooth function $S_j$ and the natural logarithm of the overall mean count for $\eta$. The algorithm was iterated until the deviance no longer decreased or for the maximum number of iterations considered.

The functionality behind GAM is the smooth function $S_i$. This approach seeks a function $f$(X) to minimise the penalised least-squares (PLS):

$$PLS = \sum_{i=1}^{n} \left[ (y_i - f(x_i))^2 - \lambda \int f''(t)dt \right] \qquad \text{(Equation 4.7)}$$

A "smooth" function will generally have a small second derivative (in absolute value), so the integral adds a "roughness penalty" to the usual least-squares function. The solution to this problem is a natural cubic spline: the function that is a cubic polynomial on the intervals defined by the $x_i$, and linear beyond the endpoints. See Silverman (1985) for an introduction and Green and Silverman (1994) for a more thorough discussion on the subject. The cubic spline was fitted using to the data points in a symmetric nearest neighbourhood containing $n_i$ points around each $x_i$.

To provide a measure of model fit, a pseudo-coefficient of determination (Swartzman et al., 1992) was calculated . This allows for a measure of the ratio of variation explained by the model to the total variation explained by both the model and any associated error. It is calculated as follows:

$$R^2 = 1 - \frac{\text{Best model residual deviance}}{\text{Overall mean or Null model deviance}} \qquad \text{(Equation 4.8)}$$

*Biomass estimates*

Once trends were estimated, these were incorporated into the generation of biomass indices. An area of general panga biomass was identified by only incorporating that area where panga were sampled over the past 14 biomass surveys. A polygon was drawn around the extreme points of the known panga distribution, forming a polygon hull. A polynomial extrapolation-interpolation algorithm (Press et al., 1989) was used on the predicted GAM point estimates to estimate predicted fish density at points not sampled but occurred within the polygon hull on a $5' \times 5'$ square grid . The point density estimates were then multiplied by the average mass per fish in each life history stage, multiplied by 25 (the area in each interpolated block) and all life history stages summed. Estimates of variance were estimated by (conditioned) bootstrap resampling with a Poisson distributed error structure and is described as follows.

Variance estimation

The (conditioned) bootstrap estimation procedure estimates the standard error of the biomass estimate $\hat{B}$ as follows. A large number ($U_{max}$) of random bootstrap samples ($X_U$: $U=1,2,\ldots,U_{max}$) were generated with the appropriate error structure (Poisson in the case of the GAM), and the set $(\hat{B}^1, \hat{B}^2, \ldots, \hat{B}^{U_{\max}})$ computed.

The variance of $\hat{B}$ was estimated by:

$$Var(\hat{B}) = \frac{1}{U_{\max} - 1} \sum_{U=1}^{U_{\max}} \left[\hat{B}^U - \overline{B}\right]^2 \qquad \text{(Equation 4.9)}$$

where $\overline{B}$ was the mean of the $\hat{B}$ vector.

The standard error for the quantity $\hat{B}$ was estimated as:

$$SE^{\hat{B}} = \sqrt{\frac{Var(\hat{B})}{n}} \qquad \text{(Equation 4.10)}$$

and the coefficient of variation of $\hat{B}$ as:

$$CV^{\hat{B}}(\%) = \frac{\sqrt{Var(\hat{B})}}{\overline{B}} \times 100 \qquad \text{(Equation 4.11)}$$

Computational time was restricted the analysis to 200 bootstrap resamples as GAM fits had to be computed for three life history stages per survey. A comprehensive review of bootstrapping can be obtained from Efron (1982), Punt (1994) and Punt and Butterworth (1993).

Finally, these estimates were compared to currently used biomass indices calculated by the Sea Fisheries Research Institute, Cape Town which uses the swept area method estimator of abundance (Badenhorst and Smale 1991).

*Optimum fishing areas*

Areas with consistently high adult and low immature biomass were determined by using Boolean logic within ArcView© using the averaged GAM predicted biomass estimates. Those areas with at least 80% or 85% spawner biomass were selected.

**Results**

A summary of all trawl survey collected and utilised in the analyses is summarised in Table 4.1. The importance of panga is highlighted on the Agulhas Bank as this species comprises 7.5% of the demersal biomass and is the third most abundant demersal species by mass (excluding the pelagic species such as the South African pilchard *Sardinops sagax*, redeye herring *Eutremeus whiteheadi* and Cape anchovy *Engraulis capensis*) surveyed since 1988 (Japp et al., 1994). Overall, the average depth surveyed was found to be similar within the spring and autumn surveys. The spring surveys tended to concentrate on slightly shallower areas, sampling the Agulhas sole *Austroglossus pectoralis*. The autumn surveys concentrated on sampling the Cape hakes *Merluccius* spp. in deeper waters. The position of the trawl stations used in the analysis between 1988 and 1995 are presented in Figure 4.1.

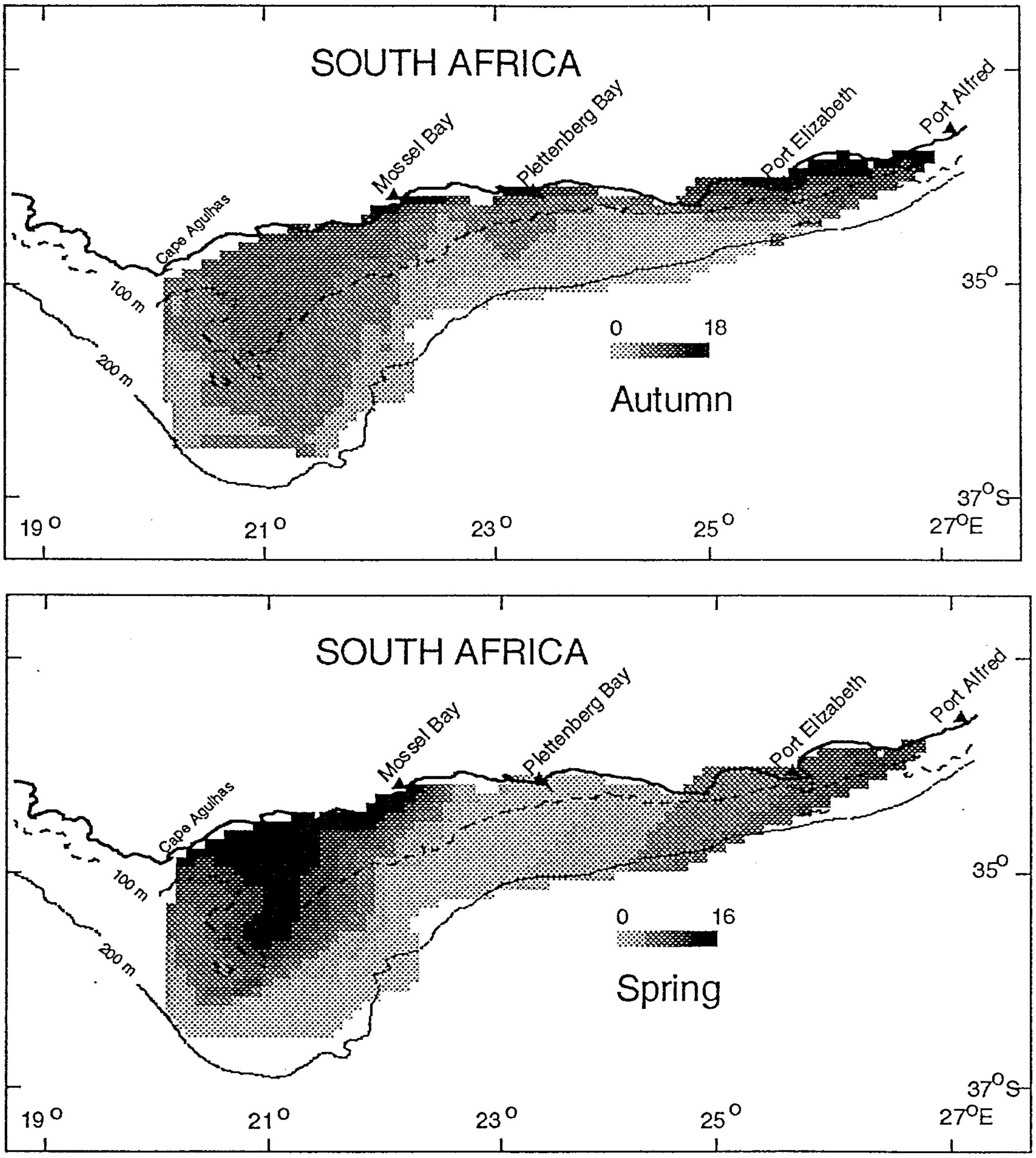

Fig. 4.3. Bottom temperature profiles (°C) for Spring and Autumn 1993 on the Agulhas Bank. The polygon coverage, represented as 5' × 5' squares, was generated by using polynomial interpolation of the raw point data.

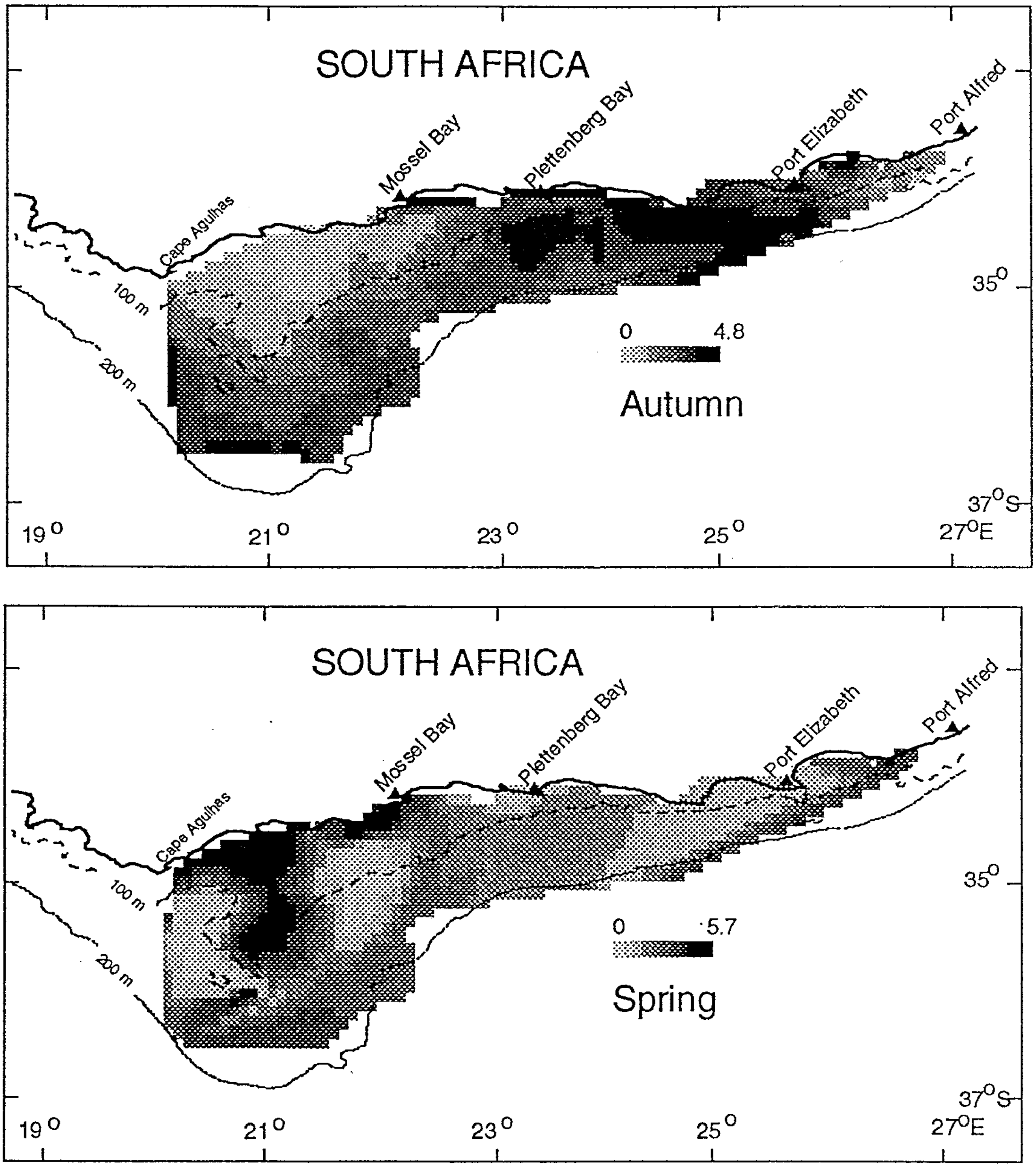

Fig. 4.4. Dissolved oxygen profiles (mg.l$^{-1}$) for Spring and Autumn 1993 on the Agulhas Bank. The polygon coverage, represented as 5' × 5' squares, was generated by using polynomial interpolation of the raw point data.

The polynomial interpolated point estimates of bottom temperature (Fig. 4.3) and dissolved oxygen levels (Fig. 4.4) provide an informative description of the physical conditions on the Agulhas Bank on a seasonal basis. Whilst only two surveys during spring and autumn 1993 have been illustrated in this study, a description of all the surveys is presented as follows. During autumn, the Eastern Agulhas Bank was the warmest, with a small coastal intrusion of warmer water on the Central Agulhas Bank. This situation was similar to the dissolved oxygen distribution with higher levels of dissolved oxygen, also being distributed on the Eastern Agulhas Bank. During winter, the intrusion on the Central Agulhas Bank from the coast to deeper areas became evident, and by spring the warmest water with the highest dissolved oxygen was widely distributed over this area. Generally, Eastern Agulhas Bank water remained relatively warm with relatively high dissolved oxygen levels.

Distinct patterns of distribution were evident within the various life history stages of panga when all trawl surveys were pooled (Fig. 4.2). Juvenile fish were distributed in a narrow area over the central Agulhas Bank within the 60 – 90 m isobath forming a nursery area. Whilst small patches of juveniles were noticeable off Mossel Bay and Plettenberg Bay, these were of low abundance. Subadult fish showed an intermediary distribution pattern between the juvenile and adult life history stages, becoming more widely distributed than the juvenile fish yet more restricted than adult fish. They were also distributed predominantly over the Central Agulhas Bank up to Plettenberg Bay, although at depths greater than juvenile fish. Adult fish were widely distributed, inhabiting deeper waters. Three distinct areas of high adult biomass were noticed, off the Central Agulhas Bank, west of Plettenberg Bay and east of Port Elizabeth. This supports anecdotal evidence from fisherman who report high spawner biomass in these areas. Changes with respect to seasonality were also evident, with fish of all life history stages inhabiting areas with higher temperatures, higher dissolved oxygen levels during the spring surveys (Table 4.2). It must be noted that whilst this form of data summary is rather cumbersome, as no suitable visualisation method has yet been developed for representing multidimensional fisheries data. Further research is soon to be initiated in this regard.

Table 4.2
Qualitative analysis of preferred zones for three physical variables obtained by visual inspection of overlaying physical and fish density coverages. Analysis was conducted for different life history stages of *Pterogymnus laniarius* on the Agulhas Bank during spring and autumn biomass surveys between 1988 and 1996

| Year | Temperature (°C) | Dissolved Oxygen (ml.l$^{-1}$) | Depth (m) | Temperature (°C) | Dissolved Oxygen (ml.l$^{-1}$) | Depth (m) |
|---|---|---|---|---|---|---|
| | | | Juveniles (< 13 cm TL) | | | |
| | | Spring | | | Autumn | |
| 1988 | - | - | - | 10.0-13.0 | 3.0-4.5 | 60-95 |
| 1989 | - | - | - | >10.0 | 2.0-4.0 | 80-90 |
| 1990 | 10.0-15.0 | >3.5 | 60-100 | >10.0 | 2.0-4.0 | 50-100 |
| 1991 | >14.0 | >4.0 | 80-100 | 9.5-13.0 | >3.0 | 70-100 |
| 1992 | >13.0 | >4.5 | 40-90 | 10.5-11.5 | 3.0-4.0 | 80-120 |
| 1993 | >14.0 | >4.8 | 60-95 | 10.0-16.0 | 3-4.3 | 60-95 |
| 1994 | >12.0 | >4.0 | 50-95 | >10.0 | 3.0-4.0 | 70-90 |
| 1995 | -[a] | -[a] | 60-100 | >10.0 | 3.0-4.0 | 60-95 |
| | | | Subadults (13-23 cm TL) | | | |
| 1988 | - | - | - | 10.0-13.0 | 2.5-5.0 | 60-120 |
| 1989 | - | - | - | >9.0 | 2.0-5.0 | 40-180 |
| 1990 | 9.0-16.0 | >3.5 | 60-200 | >9.0 | 2.0-5.0 | 40-180 |
| 1991 | >13.0 | >4.0 | 70-110 | 9.5-13.0 | >2.5 | 70-100 |
| 1992 | >10.5 | >4.0 | 50-130 | 10.5-11.5 | 2.5-5.0 | 60-130 |
| 1993 | >9.5 | >4.2 | 50-130 | 6.0-11.2 | 3.0-4.3 | 80-140 |
| 1994 | -[a] | -[a] | 60-160 | >9.5 | 2.5-4.5 | 60-180 |
| 1995 | >10.0 | 3.5-5.0 | 60-120 | 9.0-11.0 | 3.0-5.0 | 60-160 |
| | | | Adults (> 23 cm TL) | | | |
| 1988 | - | - | - | 10.0-15.0 | 2.5-5.0 | 40-180 |
| 1989 | - | - | - | >9.0 | 2.0-5.0 | 40-180 |
| 1990 | 9.0-16.0 | >3.5 | 60-200 | >9.0 | 2.0-6.0 | 50-180 |
| 1991 | >10.5 | >3.5 | 40-140 | >9.0 | >2.5 | 60-160 |
| 1992 | >10.0 | >3.9 | 50-130 | 10.0-12.0 | 2.5-5.0 | 60-180 |
| 1993 | >10 | >4.0 | 50-180 | >9.5 | 3.0-4.5 | 80-140 |
| 1994 | -[a] | -[a] | 60-180 | >9.5 | 2.5-4.5 | 60-180 |
| 1995 | >9.5 | 3.5-5.0 | 60-120 | 9.0-11.0 | 3.0-5.0 | 60-180 |

[a] Physical data too sparse for analysis.

The application of GAM allows for the investigation of the effect selected covariates have on fish density. The use of preliminary Generalized Linear Modelling, also with an underlying Poisson distribution, highlighted linear effects. Despite being statistically significant, the

GAM, incorporating the linear fits provided higher deviations with respect to the null model on all occasions resulting in the cubic splines with all covariates being used in all further analyses.

A summary of the GAM scatterplot smooths, incorporating all survey data for the three life history stages is presented in Figures 4.5 - 4.7. In all three life history stages analysed, fish density was shown to increase with longitude and decrease with respect to latitude. In juvenile fish, there was a steady increase in abundance with increased dissolved oxygen concentrations. This became less evident as fish grew larger, having little effect on the GAM smooths in the subadult and adult life history stages (Tables 4.3 - 4.5). Temperature was shown to have little effect on fish density in all life history stages. A preferred depth was clearly evident with fish moving into deeper water as they grew larger. Highest abundance occurred at <90m for juveniles, at approximately 90m for subadults and at approximately 100m for adult fish.

Table 4. 3
Non-parametric significance of various covariates to the GAM fitted to juvenile *Pterogymnus laniarius* (<13 cm TL) density.

| Year | Longitude | Latitude | Temperature | Dissolved Oxygen | Depth |
|---|---|---|---|---|---|
| | | | Spring | | |
| 1990 | <0.001 | 0.015 | <0.001 | <0.001 | <0.001 |
| 1991 | <0.001 | <0.001 | 0.162 | 0.003 | 0.022 |
| 1992 | 0.006 | <0.001 | 0.281 | 0.053 | 0.055 |
| 1993 | 0.005 | 0.009 | 0.004 | 0.093 | <0.001 |
| 1994 | 0.014 | <0.001 | 0.008 | 0.019 | <0.001 |
| 1995 | 0.005 | 0.007 | 0.048 | 0.074 | <0.001 |
| | | | Autumn | | |
| 1988 | 0.983 | 0.367 | 0.484 | 0.610 | 0.306 |
| 1989 | 0.022 | 0.249 | 0.001 | 0.467 | <0.001 |
| 1990 | <0.001 | <0.001 | 0.005 | 0.087 | 0.212 |
| 1991 | 0.137 | <0.001 | <0.001 | 0.137 | <0.001 |
| 1992 | -[a] | -[a] | -[a] | -[a] | -[a] |
| 1993 | <0.001 | <0.001 | 0.089 | 0.151 | <0.001 |
| 1994 | 0.004 | <0.001 | <0.001 | 0.025 | 0.490 |
| 1995 | <0.001 | <0.001 | <0.001 | 0.003 | 0.001 |
| All years | <0.001 | <0.001 | 0.003 | <0.001 | <0.001 |

[a] Physical data was too sparse for analysis

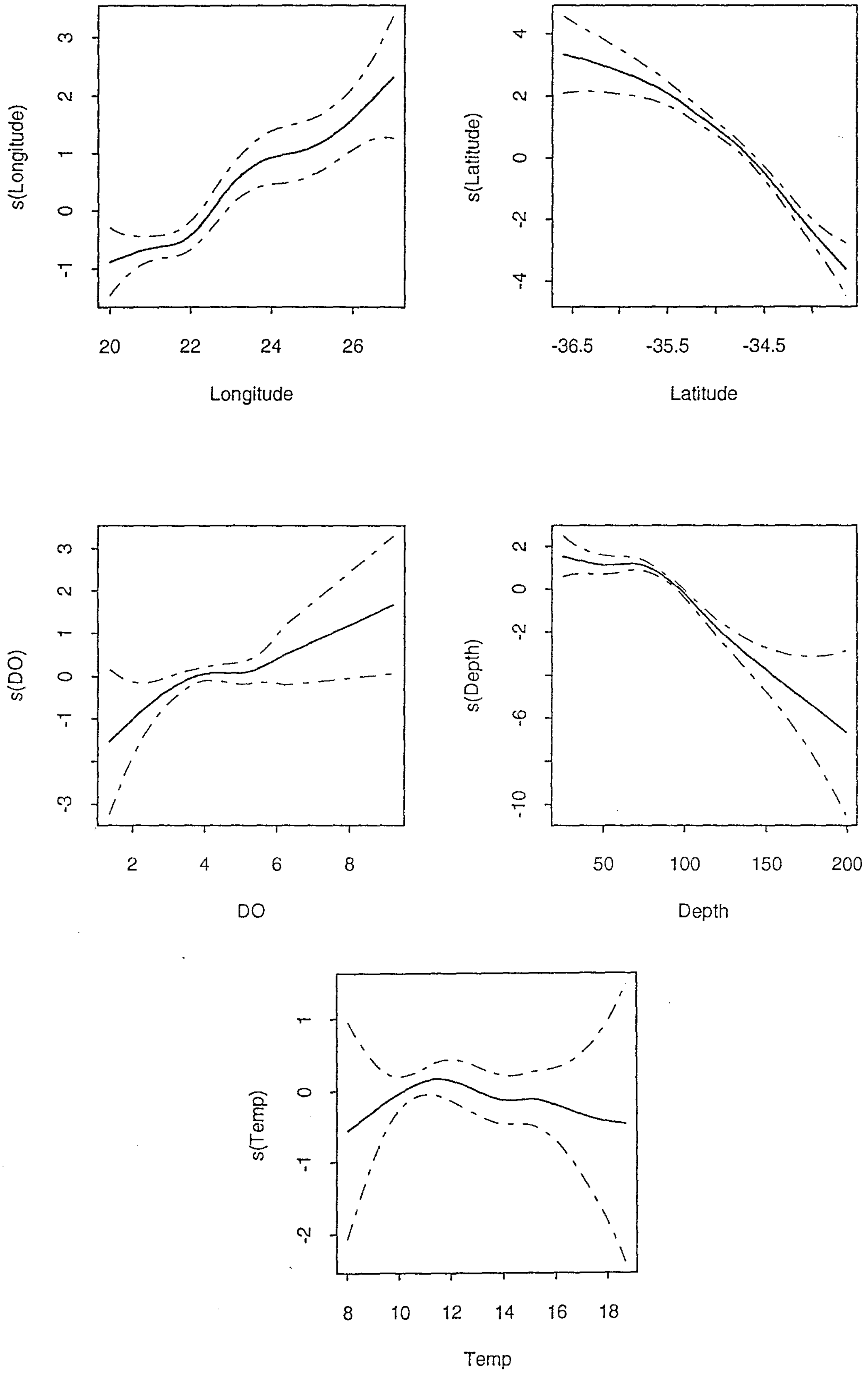

Fig. 4.5. GAM scatterplot smooths for juvenile *Pterogymnus laniarius* (<13 cm TL) density in response to various covariates for all surveys analysed between 1988 and 1995 on the Agulhas Bank. Dashed lines represent the upper and lower twice-standard-error bands.

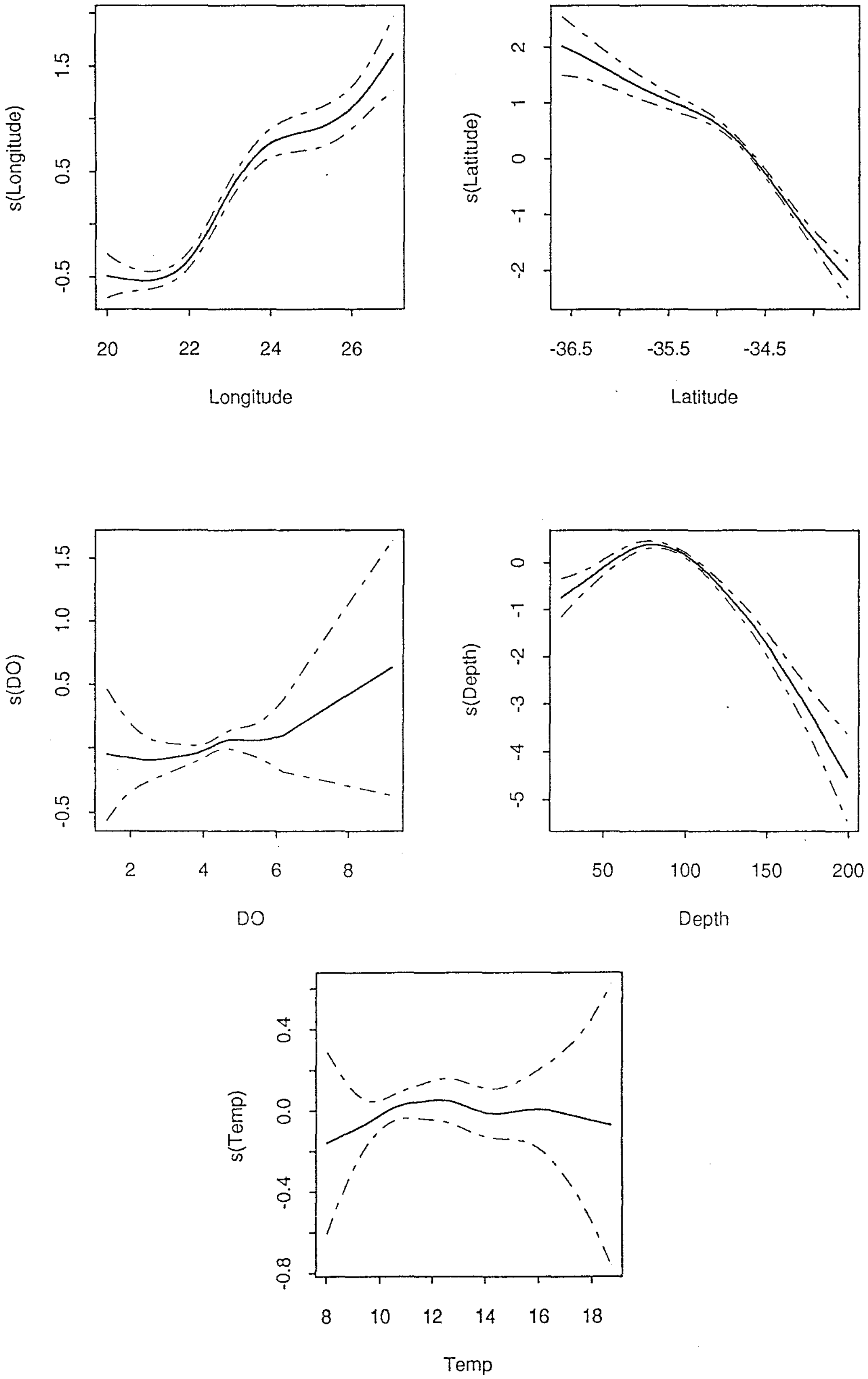

Fig. 4.6. GAM scatterplot smooths for subadult *Pterogymnus laniarius* (13-23 cm TL) density in response to various covariates for all surveys analysed between 1988 and 1995 on the Agulhas Bank. Dashed lines represent the upper and lower twice-standard-error bands.

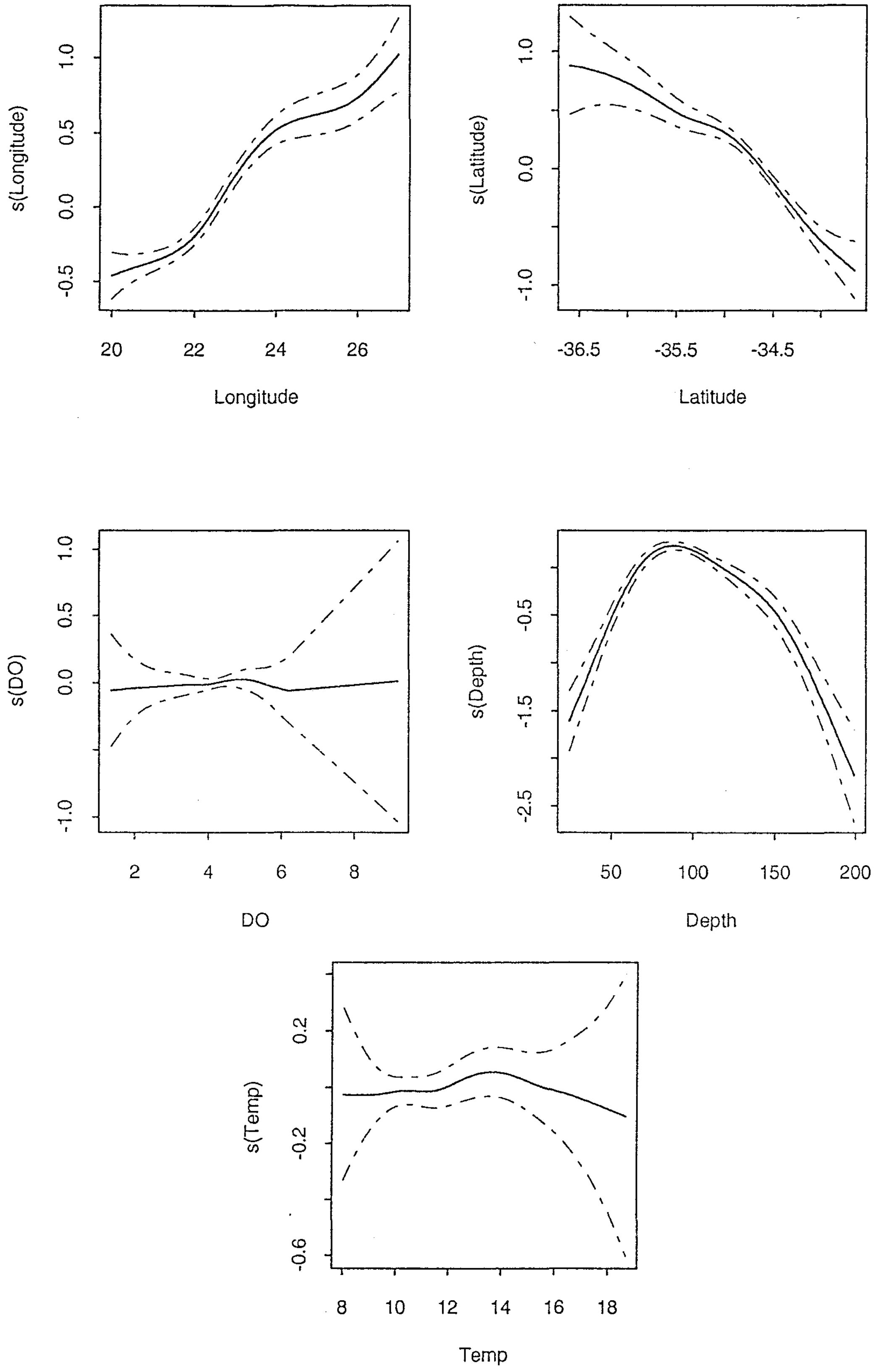

Fig. 4.7. GAM scatterplot smooths for adult *Pterogymnus laniarius* (>23 cm TL) density in response to various covariates for all surveys analysed between 1988 and 1995 on the Agulhas Bank. Dashed lines represent the upper and lower twice-standard-error bands.

Table 4.4
Non-parametric significance of various covariates to the GAM fitted to subadult *Pterogymnus laniarius* (13-23 cm TL) density.

| Year | Longitude | Latitude | Temperature (°C) | Dissolved Oxygen (mg.l$^{-1}$) | Depth (m) |
|---|---|---|---|---|---|
| | | | Spring | | |
| 1990 | <0.001 | <0.001 | 0.002 | 0.003 | <0.001 |
| 1991 | 0.004 | <0.001 | <0.001 | 0.097 | <0.001 |
| 1992 | <0.001 | 0.002 | 0.177 | 0.003 | 0.010 |
| 1993 | 0.016 | 0.005 | 0.071 | 0.277 | <0.001 |
| 1994 | 0.038 | <0.001 | 0.001 | 0.0817 | <0.001 |
| 1995 | 0.102 | <0.001 | 0.002 | 0.013 | <0.001 |
| | | | Autumn | | |
| 1988 | 0.557 | <0.01 | 0.097 | <0.001 | <0.001 |
| 1989 | 0.009 | 0.006 | 0.009 | 0.001 | <0.001 |
| 1990 | 0.028 | 0.002 | 0.185 | 0.397 | <0.001 |
| 1991 | <0.001 | 0.225 | 0.215 | 0.089 | 0.001 |
| 1992 | -[a] | -[a] | -[a] | -[a] | -[a] |
| 1993 | <0.001 | 0.145 | 0.225 | 0.273 | <0.001 |
| 1994 | 0.149 | 0.009 | 0.008 | 0.454 | <0.001 |
| 1995 | <0.001 | 0.002 | 0.002 | 0.149 | <0.001 |
| All years | <0.001 | <0.001 | 0.043 | 0.029 | <0.001 |

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[a] Physical data was too sparse for analysis

Table 4.5
Non-parametric significance of various covariates to the GAM fitted to adult *Pterogymnus laniarius* (>23 cm TL) density.

| Year | Longitude | Latitude | Temperature (°C) | Dissolved Oxygen (ml.l$^{-1}$) | Depth (m) |
|---|---|---|---|---|---|
| | | | Spring | | |
| 1990 | 0.104 | <0.001 | <0.001 | 0.212 | <0.001 |
| 1991 | 0.458 | 0.001 | 0.387 | 0.047 | <0.001 |
| 1992 | 0.136 | 0.177 | 0.124 | 0.165 | <0.001 |
| 1993 | 0.030 | 0.231 | 0.020 | 0.047 | <0.001 |
| 1994 | 0.110 | 0.063 | <0.001 | 0.025 | <0.001 |
| 1995 | 0.071 | <0.001 | 0.005 | 0.614 | <0.001 |
| | | | Autumn | | |
| 1988 | 0.097 | 0.009 | 0.132 | 0.839 | <0.001 |
| 1989 | 0.353 | <0.001 | 0.008 | 0.195 | <0.001 |
| 1990 | 0.015 | <0.001 | 0.324 | 0.007 | <0.001 |
| 1991 | 0.257 | 0.040 | 0.247 | 0.177 | <0.001 |
| 1992 | -[a] | -[a] | -[a] | -[a] | -[a] |
| 1993 | 0.009 | 0.229 | 0.084 | 0.121 | <0.001 |
| 1994 | 0.024 | 0.723 | 0.238 | 0.255 | <0.001 |
| 1995 | <0.001 | 0.008 | 0.012 | 0.003 | <0.001 |
| All years | <0.001 | <0.001 | 0.227 | 0.321 | <0.001 |

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[a] Physical data was too sparse for analysis

Non-parametric statistical significance of the various covariates using an appropriate $\chi^2$ statistic (Hastie and Tibshirani, 1990) for each life history stage and survey analysed is summarised in Tables 4.3 - 4.5 .

In the juvenile dataset, four of the five covariates used in the analysis showed a consistent significant effect on the GAM. Whilst latitude and longitude consistently illustrated the presence of a nursery area on the Central Agulhas Bank, the significant effects of these covariates appear to be merely descriptive. Dissolved oxygen, generally had an insignificant effect in determining the density of juveniles with one third of the surveys analysed being significant. In contrast, both depth and temperature were significant in most surveys. A similar trend was evident with the subadult fish. Both dissolved oxygen and temperature were generally insignificant in the adult GAM. The eurytopy of the adult fish was stressed, with mature fish appearing to be able to tolerate a wider range of physical conditions. This, therefore, provides the mechanism for adult fish to be able to move eastwards and colonise vast areas of the Eastern Agulhas Bank. In all life history stages, depth was found to be highly significant in all the surveys analysed.

The best GAM fits which include the rotation of latitude and longitude co-ordinates to be corrected for directional invariance or isotropy (Swartzman et al., 1992) are summarised in Table 4.6. Generally, the angles of rotation were low and similar within each survey modelled. The pseudo-$r^2$ were generally high in the juvenile fish which have a distinct nursery area of the Central Agulhas Bank and are the most stenotopic, preferring a narrower range of physical conditions. GAM fits to the adult dataset exhibited the poorest fits due to the adult fishes being eurytopic, having the ability to utilise and inhabit large areas of the Bank. GAM fits to the subadult data were intermediate between those of the juvenile and adult life history stages. Average GAM estimates of biomass for all three life history stages are presented in Figure 4.8.

Table 4.6
Pseudo-coefficients of determination ($r^2$) and angle of rotation of the latitude and longitude co-ordinates (angle from clockwise from North) for the best fitting GAM fits. Data are summarised for three life-history stages of *Pterogymnus laniarius* sampled on the Agulhas Bank during biomass survey cruises from 1988-1996.

| | Spring /Summer surveys | | | | | | Autumn /Winter surveys | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Juveniles | | Subadults | | Adults | | Juveniles | | Subadults | | Adults | |
| Year | $r^2$ | Angle | $r^2$ | Angle | $r^2$ | Angle | $r^2$ | Angle | $r^2$ | Angle | $r^2$ | Angle |
| 1988 | - | - | - | - | - | - | 0.99 | 5 | 0.61 | 1 | 0.59 | 1 |
| 1989 | - | - | - | - | - | - | 0.85 | 1 | 0.57 | 1 | 0.63 | 1 |
| 1990 | 0.65 | 1 | 0.57 | 9 | 0.60 | 9 | 0.63 | 14 | 0.56 | 9 | 0.53 | 9 |
| 1991 | 0.67 | 1 | 0.57 | 7 | 0.58 | 11 | 0.70 | 5 | 0.55 | 1 | 0.49 | 3 |
| 1992 | 0.90 | 7 | 0.44 | 3 | 0.41 | 6 | 0.90 | 7 | 0.39 | 1 | 0.44 | 3 |
| 1993 | 0.76 | 2 | 0.58 | 8 | 0.47 | 7 | 0.71 | 4 | 0.64 | 4 | 0.56 | 3 |
| 1994 | 0.52 | 1 | 0.59 | 1 | 0.69 | 1 | 0.76 | 11 | 0.67 | 11 | 0.64 | 1 |
| 1995 | 0.61 | 1 | 0.42 | 4 | 0.54 | 15 | 0.69 | 8 | 0.64 | 2 | 0.53 | 9 |

Figure 4.9 illustrates, and Table 4.7 summarises, the GAM predicted and currently used estimates of biomass. Estimates are presented together with their coefficients of variation. The GAM predicted biomass estimates were remarkably similar to those of the swept area estimates used by the Sea Fisheries Research Institute, Cape Town. Using both biomass estimation methods, biomass increased between 1988 and 1996. The rate of increase was slightly lower for the GAM estimates, which were more stable and exhibited less variability. During spring and autumn at least 60% of the spawner biomass was situated over the Central Agulhas Bank (Table 4.8).

Those areas suitable for commercial exploitation, comprising of at least 80% spawner biomass, are presented in Figure 4.10. In both the scenarios presented, the Eastern Agulhas Bank consistently contained the highest proportion of spawner biomass due to its distance from the nursery area on the Central Agulhas Bank. If the proportion of spawner biomass was specified to be >85%, the model only selected the eastern and western edge of the

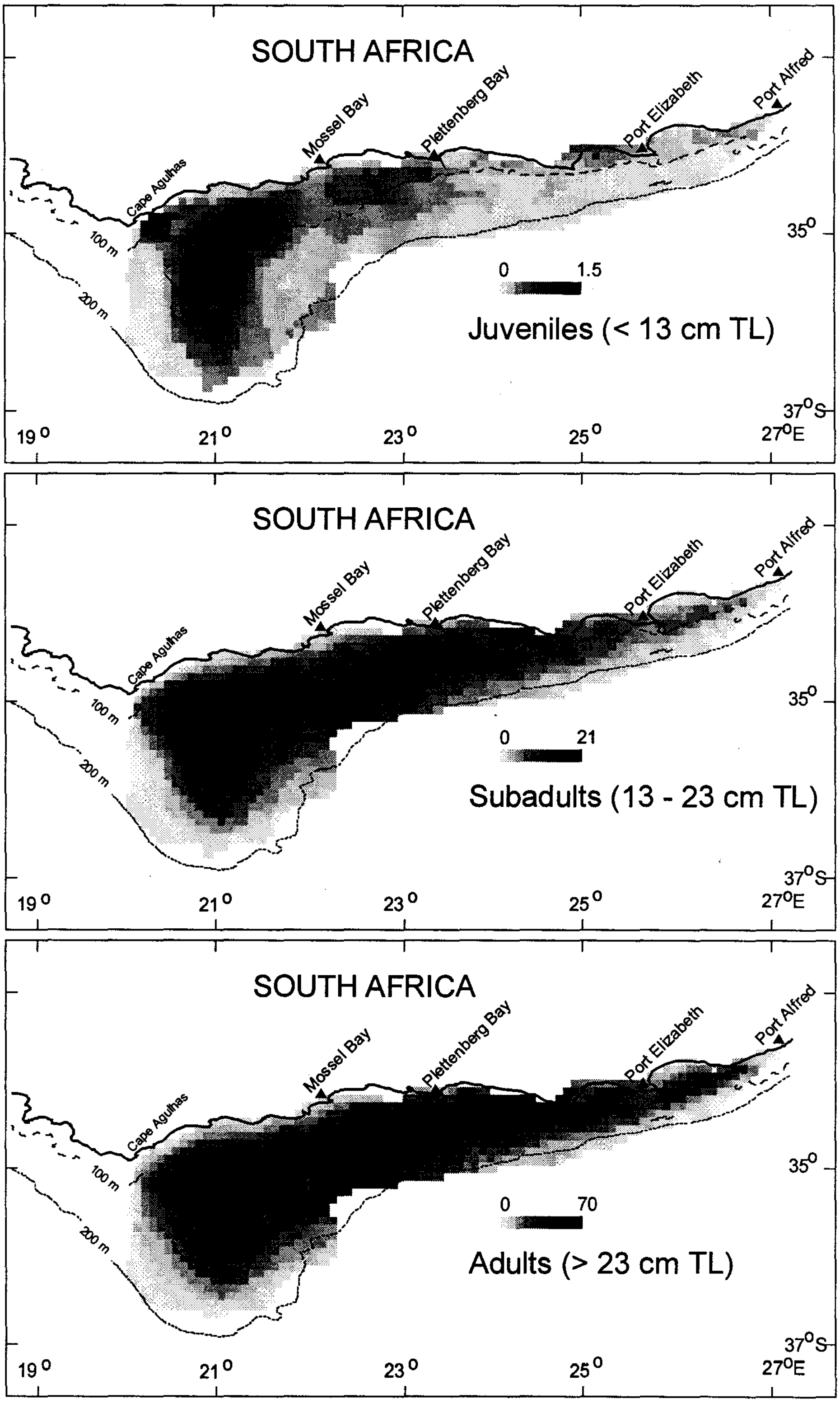

Fig. 4.8. Average GAM predicted fish biomass (metric tons) for three life history stages of *Pterogymnus laniarius* on the Agulhas Bank.

Central Agulhas Bank. When the criteria for area selection was reduced to contain only those areas with >80% spawner biomass, a larger portion of the Agulhas Bank was chosen. In both scenarios, the high juvenile and subadult abundance on the mid Central Agulhas Bank excluded these areas as suitable for fishing effort.

## Discussion

From the data presented, it appears that the panga has a distinct ontological shift in distribution with respect to size and age. This is noticable in the distinct nursery area for immature fish over the Central Agulhas Bank.

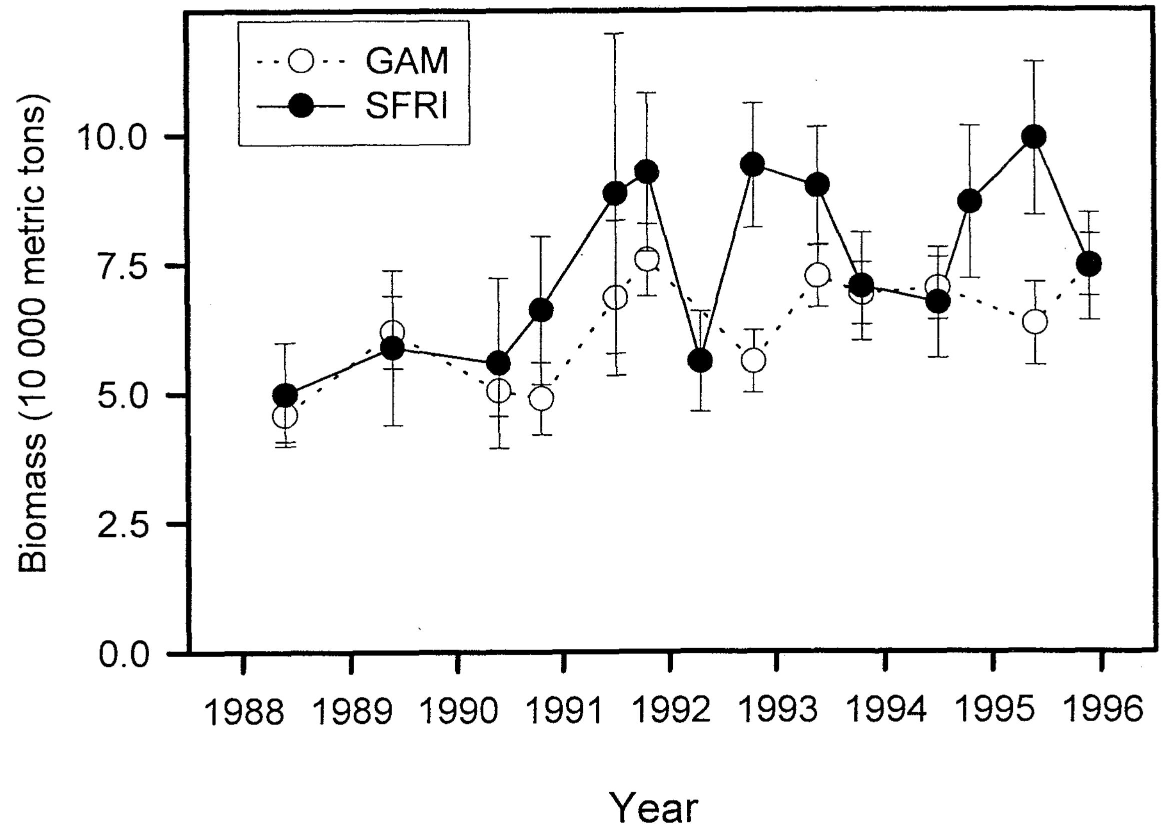

Fig. 4.9. Biomass estimates (± one standard error) for *Pterogymnus laniarius* using the currently used SFRI and GAM predicted estimates from this study between 1988 and 1995.

Table 4.7
Biomass indices with coefficients of variation using two estimation methods for *Pterogymnus laniarius* on the Agulhas Bank, South Africa from 1987-1997. The method currently used by the Sea Fisheries Research Institute, Cape Town (SFRI) is based on a standard randomised depth stratified, swept area estimator. The GAM method is the one described in this study. The percentage annual change in the biomass indices using each method is reflected in the statistic *SLOPE* which is calculated by dividing the slope of a least-squares regression fitted to the biomass series and dividing it by the average biomass over the study period.

| | Spring/Summer surveys | | | | Autumn/Winter surveys | | | |
|---|---|---|---|---|---|---|---|---|
| | SFRI | | GAM | | SFRI | | GAM | |
| Year | Point Est. | CV (%) | Point Est. | CV (%) | Point Est. | CV (%) | Point Est. | CV (%) |
| 1988 | - | - | - | - | 49.84 | 20.1 | 45.75 | 15.1 |
| 1989 | - | - | - | - | 58.85 | 25.4 | 61.86 | 16.3 |
| 1990 | 66.09 | 21.7 | 48.97 | 15.4 | 55.82 | 29.5 | 50.45 | 18.3 |
| 1991 | 92.69 | 16.5 | 75.78 | 8.6 | 88.6 | 34.9 | 68.44 | 20.7 |
| 1992 | 93.95 | 12.8 | 56.05 | 5.3 | 56.11 | 17.3 | -[a] | -[a] |
| 1993 | 70.54 | 14.8 | 69.17 | 7.5 | 89.96 | 12.6 | 72.45 | 7.3 |
| 1994 | 86.72 | 17.0 | -[b] | -[b] | 67.37 | 15.9 | 70.18 | 10.4 |
| 1995 | 74.33 | 14.0 | 74.64 | 8.0 | 99.04 | 14.9 | 63.34 | 7.4 |
| *SLOPE* | 0.0 | | 5.7 | | 7.7 | | 4.4 | |

[a] - no convergence in GAM; [b] - not enough coverage of bank for effective interpolation

Results obtained from both the qualitative and quantitative methods used were similar. The combined trends, therefore, provide a reasonable indication of the functional relationship between the abundance of fish and it's predictive covariates. It was noted that in immature fish, density was significantly effected by both temperature and depth. In mature fish, only depth provided a significant effect (with the exception of the spatial covariates) to the GAM fit. Dissolved oxygen was found to be insignificant in the subadult and adult life history stages and was probably due to the relatively high dissolved oxygen levels over the entire Agulhas Bank. This is in contrast to the upwelling dominated Benguela system where anoxic conditions can prevail (Smale et al., 1993; Roberts and Sauer, 1994). Whilst there appears to be some correlation between temperature and depth (with temperature decreasing with depth), depth was a consistently significant effect in all the GAM fits. It is, therefore, suggested that depth is a primary factor determining the abundance of panga on the Agulhas Bank. Similarly, depth was the covariate that was found to determine flatfish abundance in the Bering Sea (Swartzman et al., 1992) and gadoid and flatfish species on the Georges Bank (Murawski and Finn, 1988). These results, therefore, support the depth stratification methodology employed in current biomass estimation surveys and possibly accounts for the similarity in abundance estimates between the two biomass estimators compared in this study. It could also be argued that due to the strong correlation between latitude and depth, the predictability of the model could be improved by reducing the number of model covariates, in this case depth. A step-wise regression reduction procedure found that all covariates were important to the GAM (Tables 4.3 - 4.5). This was principally due to the triangular shape of the Agulhas Bank and suggested that all covariates (including latitude) should be retained within the GAM.

Table 4.8
Proportion of spawner biomass that is situated over the central (20° - 23°E) and eastern (23° - 27°E) portions of the Agulhas Bank. Estimates were calculated using the GAM predicted estimates of biomass.

| | Spring/Summer surveys | | Autumn/Winter surveys | |
|---|---|---|---|---|
| | Central Bank | Eastern Bank | Central Bank | Eastern Bank |
| 1988 | - | - | 0.35 | 0.65 |
| 1989 | - | - | 0.64 | 0.36 |
| 1990 | 0.63 | 0.37 | 0.50 | 0.50 |
| 1991 | 0.57 | 0.43 | 0.63 | 0.37 |
| 1992 | 0.57 | 0.43 | - | - |
| 1993 | 0.66 | 0.34 | 0.67 | 0.33 |
| 1994 | - | - | 0.66 | 0.34 |
| 1995 | 0.56 | 0.44 | 0.65 | 0.35 |
| Average | 0.60 | 0.40 | 0.59 | 0.41 |

The question still arises why small, immature fish are distributed over the Central Agulhas Bank. If depth were the principal factor in determining abundance, their distributional range should include the entire Agulhas Bank. A similar question arises as to why the larger fish move eastwards after sexual maturation. These questions stress the use of exploratory data analysis using generalised statistical and spatial methods which allow for trends to be observed before hypotheses are formulated.

If both surface and bottom current profiles presented in Figure 2.1 together with the panga's reproductive biology are considered, an alternate scenario can be illustrated. Panga has been shown to have a non-seasonal breeding pattern with all mature individuals spawning throughout their distributional range throughout the year (Chapter 3).

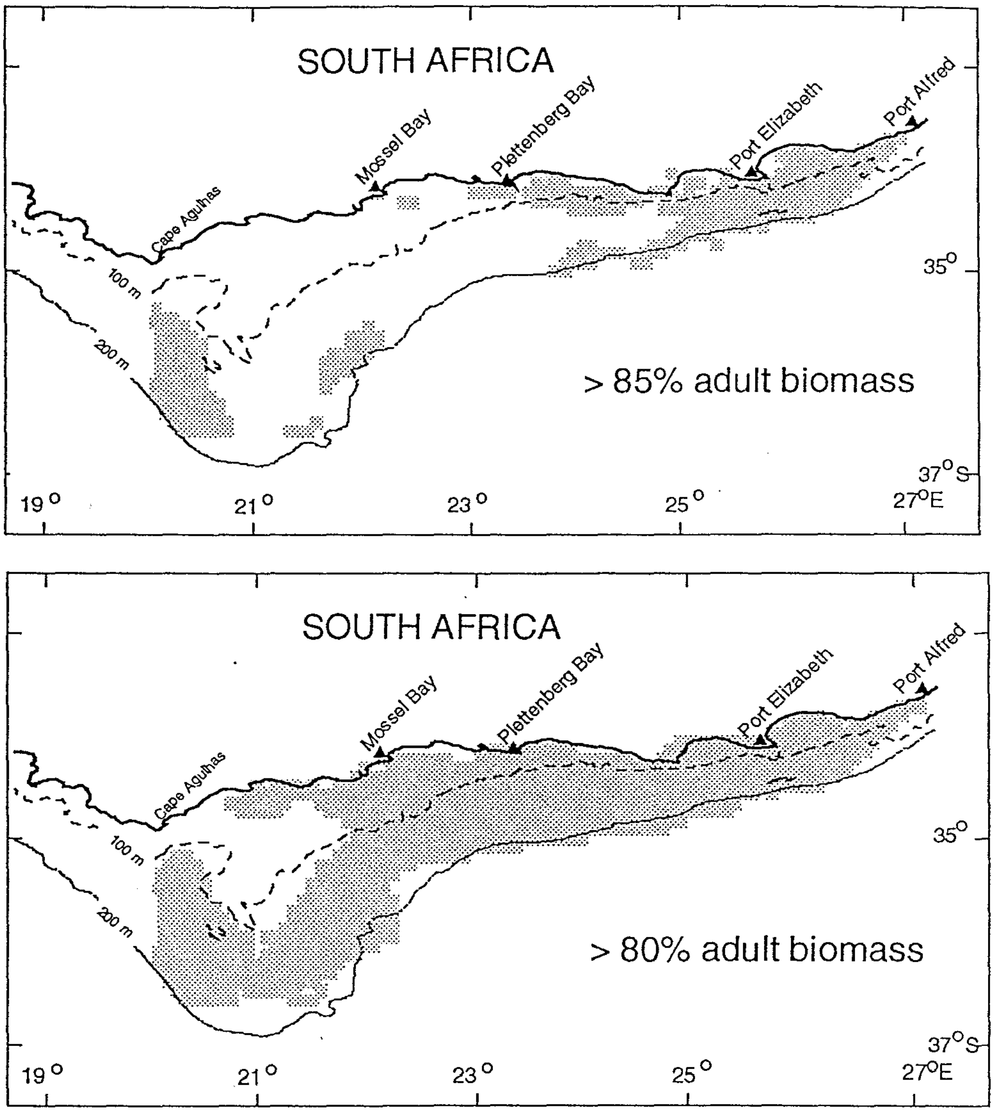

Fig. 4.10. Optimum areas to fish *Pterogymnus laniarius* which minimises the impact on juvenile fish whilst directing effort towards spawner biomass. The hashed areas represents those areas where the total biomass is comprised of at least 80% adults and at least 85% adults. Data used in the analysis were GAM biomass estimates which were pooled and averaged for all surveys between 1988-1995.

Spawned eggs and pre-metamorphosed planktonic larvae from eastward distributed spawning adults would, therefore, be carried westwards by the Agulhas Current before being advected to the coast by the anti-cyclonic gyre over the Central Agulhas Bank. Similarly, eggs and larvae from Central Agulhas Bank spawning adults would merely be advected towards the coast. This is similar to the conclusions presented by Werner et al. (1993) using a 3D circulation model which in part explained the distribution of cod and haddock larvae on the George's Bank. High copepod densities in the cool upwelling ridge would, in addition, provide a suitable food source for the planktonic larvae. The decrease in surface current strength over the Central Agulhas Bank could provide a concentration zone for post-metamorphosed larvae and the decreased bottom current strength would prevent fish from being moved far from their deposition site and lost to the Benguela system. As the fish grow and mature, they become large enough to tolerate stronger currents and also have the ability to feed to on a greater variety of hard-shelled prey. As a density-dependent response, adult fish would reduce conspecific competition and move eastwards to colonise larger areas of suitable habitat. Overall, panga would restrict themselves to a specific depth range to avoid stress associated with shallow, coastal wind-driven upwelling and the strong Agulhas current with its shelf-break induced upwelling (Lutjeharms et al., 1996).

It has been shown in a variety of studies that the distribution of populations is strongly determined by some underlying habitat association, preferred physical conditions, proximity to food sources or areas where spawning success will be maximised (Murawski and Finn, 1988; Mahon and Smith, 1989; D'Amours, 1993; Perry and Smith, 1994; Le Clus et al., 1994; 1996). In South Africa, there is paucity of knowledge on the habitat types and the habitat preferences of associated fish assemblages on the Agulhas Bank. Whilst it is known that there are extensive areas of hard, low-profile reef (Badenhorst and Smale, 1991; Smale et al., 1993;

Le Clus et al., 1996) which appears to be the preferred habitat for panga, there is a distinct need for this information. Data that is available is restricted to surficial sedimentary deposits (Le Clus et al., 1996). In this regard, a concerted effort is needed in this area before the spatial distribution of any species inhabiting the Agulhas Bank can be fully understood. GIS technology offers the facility to combine many biological datasets and relate them to system-wide observations of habitat. Furthermore as habitat is not the resource of value, relating biological consequences to the habitat allows for the ease of management of the habitat via their biological indicators. In the case of the Agulhas Bank, as more habitat information becomes available together with improved knowledge of their associated fish assemblages, it can be added as a new coverage to the GIS. The updated GIS can then be easily reanalysed and interpreted. As a result, the spatial distribution and abundance of panga will become more fully understood. Understanding the influence of the marine environment, a knowledge of the habitat types and preferences can, therefore, facilitate better management of panga and other sympatric species.

The spatial trends that have been highlighted can be incorporated into the generation of biomass estimates (Swartzman et al., 1992). From the GAM biomass estimates, a slight increase in the biomass of the panga stock over the past decade was noticable. Application of an age-structured production model in Chapter 6 showed that this recovery is probably a response to the decreased fishing effort over the past 20 years. Whilst it would be expected that the stock should rebuild at a faster rate given the low fishing pressure, a combination of the low productivity of the stock resulting from a low growth rate, low natural mortality and a relatively high longevity, would delay rapid rebuilding. There are two factors that make the GAM derived biomass point estimates more constant than the SFRI estimates in addition to their reduced variability. Firstly, the smooth of the GAM tends to reduce the extremely large counts at individual stations. The GAM estimate is, therefore, analogous to other robust estimators such as the trimmed mean, which downplays the effect of large individual points which would strongly influence the abundance estimate. Secondly, the GAM includes the effect of trends in abundance due to model covariates. There is also concern regarding the strength of the spatial structure of the trawl surveys and whether or not there is an improvement in the estimation of abundance over currently used estimators. The averaging effect of the GAM could, therefore, merely mask any significant changes in biomass within the years analysed. It is for this reason that SFRI estimates should be used in the short term, until simulations can provide results as to whether or not the GAM abundance estimates are preferable.

Optimal management areas can be obtained by selecting those areas which are the most suitable for fishing. Using a GIS, the biomass of the stock can be easily disaggregated by region or life history stage, thereby facilitating and improving dynamic pool modelling. The most suitable areas would, therefore, include those in which fishing effort (and hence fishing mortality) is reduced on vulnerable life history stages. These would include immature fish which have a discrete nursery areas or annual migrations of spawner biomass to specific spawning areas. In case of the panga, only the former constraint applies as adult fish spawn throughout the year throughout their distributional range (Chapter 3). As panga is also caught predominantly as bycatch in the demersal trawl optimal areas for harvesting should also include most of the areas fished by the existing demersal trawl fleet. This includes most of the Agulhas Bank. In both optimum fishing scenarios presented in this study, the fleet should merely be restricted from fishing on the mid Central Agulhas Bank area.

The use of spatial analysis to identify trends in fish distribution and abundance and to incorporate trends in assessment models and fisheries management is obvious. Similarly, a GIS has enormous value for organising biological data and discovering their underlying relationships. This is a result of each biological data set being only one temporary value because it is a specific sample drawn from a population or community that is highly variable in both time and space. Despite noticing the potential of GISs, Meaden and Kapetsky (1991), Simpson (1992) and Meaden (1996) noted that they have not been fully utilised, instead, being restricted to terrestrial or freshwater applications. This is primarily a response to high costs associated with the collection of marine biological, physico-chemical and sedimentation data and in synthesizing the vast databases available into a compatible and comparable format (Caddy and Garcia, 1986; Meaden, 1996). A GIS includes a complex technology that can enhance the utility of diverse data at both regional or larger scales. By simultaneously understanding the exploitation patterns and the distribution and abundance of the resource on a spatial and temporal scale, effective resource management can be facilitated. A GIS can, therefore, improve fisheries management decisions including the introduction of best management practices, integrated environmental management (Li and Saxena, 1993) and intelligent GIS (Coulson et al., 1987). For the reasons mentioned above, the results from this study are being used in the development of a larger Fisheries Information System including the spatial analysis of all other sympatric species and the fishing patterns on the Agulhas Bank. Each spatially referenced dataset will be used as a compatible coverage to allow for the development of a new modelling paradigm to simultaneously manage the resources in question and the fisher communities that exploit them.

# Chapter 5 - Management options for the panga using per-recruit models

## Introduction

The assessment of bycatch species has often been hampered by a lack of directed catch and effort data, insufficient catch-at-age and other biological data pertinent to the application of age based models. Data available are often imprecise and of little quantitative value. It is these problems which point to the use of an abbreviated version of the full dynamic pool model, the yield-per-recruit model (Beverton and Holt, 1956; 1957). This model has been widely applied in the management of reef fisheries in the past due to similar problems regarding their management (Huntsman et al., 1983; Bannerot et al., 1987; Pulfrich and Griffiths, 1988b; Buxton, 1992; Punt et al., 1993). The advantage of per-recruit models in the development of a management strategy is that they allow for easy evaluation of the response of yield-per-recruit to changes in fishing mortality and age-at-50%-selectivity, two fundamental control measures in managing a fishery. This allows for management advice to be obtained without the exact relationship between effort and fishing mortality being known.

The panga resource has been assessed in the past using surplus production models based on effort data from the late 1960's to 1970's, and yield-per-recruit models using growth and mortality data from scale based ageing (Sato, 1977; 1980). As already stated, ageing of long lived species using scales, has been shown to be inaccurate in long-lived species as it tends to underestimate longevity, resulting in the overestimation of mean lengths at age and growth rates (Chapter 3). The re-estimation of age, growth and mortality rates using sectioned otoliths in this study revealed that growth was substantially slower than previous estimates (Chapter 3). This chapter presents a reassessment of the stock and presents management options, based on a per-recruit analysis.

## Materials and Methods

Data used in the analysis were collected using the methods described in Chapter 2 whilst the parameter estimates used in the models were obtained in Chapter 3. These parameters are summarised in Table 5.1. To assess the sensitivity of the various per-recruit models to a possible error in the natural mortality estimates two natural mortality scenarios were considered. These corresponded to the estimate obtained in Chapter 3 and Sato's (1980) natural mortality estimate of $M$ = 0.20 year$^{-1}$. The range of natural mortality estimates chosen, therefore, incorporates a large proportion of the estimates obtained using the empirical models analysed in Chapter 3.

Table 5.1
Parameter estimates used in the per-recruit analysis of *Pterogymnus laniarius* on the Agulhas Bank. Parameters used in the sensitivity analyses are shown in parentheses.

| Parameter | Estimate |
|---|---|
| $L_\infty$ | 379.35 mm FL |
| $K$ | 0.13 year$^{-1}$ |
| $t_0$ | -1.78 years |
| $e^*$ | 0.00002 g |
| $f^*$ | 3.031 |
| $M$ | 0.20; 0.28 year$^{-1}$ |
| $F$ | 0.16; 0.08 year$^{-1}$ |
| *Max* | 20 years |
| $a_{50}$ | 5.5 years (7.3; 4; 2.5 years) |
| $\delta_{50}$ | 0.6 year$^{-1}$ (knife-edged selection; 0.9) |
| $a_m$ | 4 years (2.5; 5.5 years) |
| $\delta_m$ | 0.6 year$^{-1}$ |

$^*$ *e* and *f* are the parameters that define the length-mass relationship

The selectivity pattern for each fishing sector was assumed to be time invariant, having the logistic form

$$S_a = \frac{1}{1+e^{-(a-a_{50})/\delta}}$$

where $S_a$ is the selectivity of the gear on a fish of age $a$, $a_{50}$ is the age-at-50%-selectivity and $\delta$ is the parameter which determines the width of the age-specific selectivity function. The ogive was fitted to the ascending limb of the inshore trawl and offshore linefishery cumulative age-frequency data (Fig. 5.1). The model parameters were estimated by minimising the squared difference between the observed and predicted selectivity values. The mode of the age-frequency distribution was taken to represent 100% selectivity. These results are similar to Uozumi et al. (1985) who conducted covered cod-end experiments in a previous trawl net selectivity study. The proportion of sexually mature fish at age *a* was obtained using a logistic function of the same form discussed in Chapter 3.

Yield-per-recruit (*YPR*) and spawner biomass-per-recruit (*SBR*) as a function of fishing mortality $F$ were determined as:

$$YPR_F = \sum_{a=0}^{max} w_{a+1/2}\, S_a\, F\, \tilde{N}_a [1 - e^{-(M+S_a F)}] / (M + S_a F)\ \Delta a \qquad \text{(Equation 5.1)}$$

$$SBR_F = \sum_{a=0}^{max} \beta_a w_a \tilde{N}_a\ \Delta a \qquad \text{(Equation 5.2)}$$

and Biomass-per-recruit (*BR*) as a function of age was determined as:

$$BR_a = w_{a+1/2} \tilde{N}_a \qquad \text{(Equation 5.3)}$$

$\tilde{N}_a$, the relative proportion of fish at age *a,* is defined as

$$\tilde{N}_a = \begin{cases} 1 & \text{if } a = 0 \\ \tilde{N}_{a-1}\, e^{-(M+S_{a-1}F)} & \text{if } 1 \le a < max \\ \tilde{N}_{max-1}\, e^{-(M+S_{max-1}F)} / (1 - e^{-(M+S_{max}F)}) & \text{if } a = max \end{cases} \qquad \text{(Equation 5.4)}$$

where $w_a$ is the mass of fish at age *a*, $S_a$ is selectivity-at-age *a*, $F$ is the instantaneous rate of fishing mortality on fully recruited cohorts, $M$ the rate of natural mortality, $\beta_a$ the proportion of mature fish at age *a* and *max* the lumped plus-group (Butterworth et al., 1989). A lumped plus-group was used as it was possible that fish >16 years could exist in the population due to the heavily calcified nature of the otoliths which made age interpretation of old fish difficult. This specification, however, has little effect on the analyses. All summations were conducted with a step size ($\Delta a$) of 1/10th of a year.

Four Target Reference Points (*TRPs*) were investigated from the yield-per-recruit and spawner biomass-per-recruit curves. $F_{max}$ the fishing mortality which corresponded to the maximum of the yield-per-recruit curve, $F_{0.1}$ or marginal yield value (Gulland and Boerema, 1973) where the slope of the yield-per-recruit curve is 10% of that at the origin, and $F_{SB50}$ and $F_{SB40}$ the fishing mortalities corresponding to a reduction in the spawner biomass-per-recruit curve to 50% and 40% of its unexploited equilibrium level, respectively. Estimates of yield were obtained by multiplying the *YPR* estimates by an estimate of pristine 0-year recruitment obtained from Sato's (1980) cohort analysis. Using both natural mortality scenarios of $M$ = 0.28 year$^{-1}$ and $M$ = 0.20 year$^{-1}$, pristine 0-year old recruitment was estimated back from Sato's (1980) estimate of 1-year old fish at 77 million and 71 million recruits, respectively. This was calculated by dividing the number of 1-year old fish by $e^{-M}$ as $N_0e^{-M} = N_1$, where $N_0$ and $N_1$ are the number of 0- and 1-year old fish, respectively.

The sensitivity of the yield-per-recruit and spawner biomass-per-recruit models to changes in various input parameters was assessed. The model parameters chosen for the sensitivity analysis were the age-at-50% selectivity, the steepness of the selectivity function and the age-at-50%-maturity (Table 5.1). These changes represent selection into the offshore linefishery, selection into the foreign trawlfishery (Sato, 1980), a knife-edged selectivity pattern and scenarios where age-at-maturity occurs before or at the age-at-50%-selectivity.

## Results

Length and age frequency distributions of fish sampled in the inshore trawlfishery and offshore linefishery are described in Figure 5.1. Fish are first caught in both fisheries at 4 years of age and are fully selected by 7 and 9 years of age in the inshore trawl and linefisheries respectively. Age-at-50%-selectivity ($a_{50}$) was estimated at 5.5 years for the inshore trawlfishery and 7.3 years for the linefishery (Table 5.1). The mean lengths of fish caught were 27 cm FL and 29 cm FL in the inshore trawl and offshore linefisheries respectively. Selectivity was more apparent in the offshore linefishery, where larger fish were targeted than in the inshore trawlfishery where a wider range of age classes were caught.

### *Per-recruit analysis*

An isopleth diagram describing the response of yield-per-recruit to different values of fishing mortality ($F$) and age-at-50%-selectivity ($a_{50}$) is presented in Figure 5.2. The response isopleth showed that yield-per-recruit increased rapidly at low values of $F$ over most of the range of $a_{50}$. At small values of $a_{50}$ , maximum yield-per-recruit was attained at correspondingly low values of $F$, above which yield-per-recruit decreased gradually. From $a_{50}$ ranging between 2 and 7 years, maximum yield-per-recruit was undefined for $F > 0.3$ year$^{-1}$. At values of $a_{50} >$ 9 years, the asymptotic yield-per-recruit was attained with low values of $F$.

Figure 5.3 illustrates the expected biomass-per-recruit for fished and unfished populations of panga. In all scenarios, the biomass-per-recruit of fish surviving past the age-at- 50%-selectivity decreased rapidly, a trend common in slow-growing fishes (Ricker, 1963; Buxton, 1992).

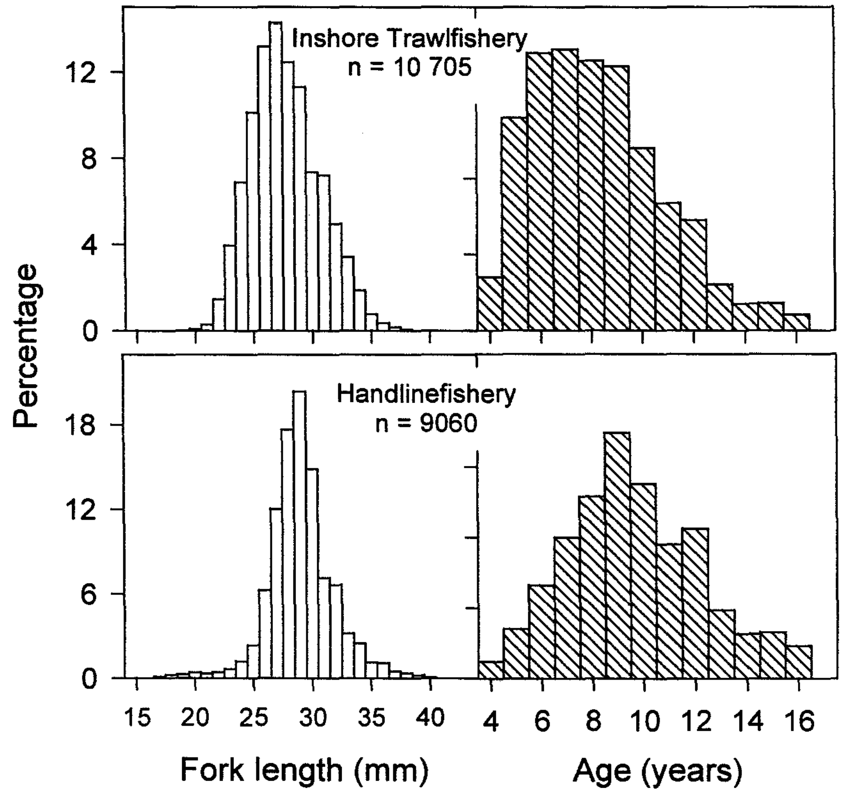

Fig. 5.1. Length and age frequency distributions of *Pterogymnus laniarius* sampled on the Agulhas Bank from the inshore trawl and offshore linefisheries between 1993 and 1994 .

Yield-per-recruit and spawner biomass-per-recruit are shown in Fig. 5.4. In both natural mortality scenarios, the level of fishing effort required for a marginal yield ($F_{0.1}$) strategy was slightly higher than the effort needed to reduce spawner biomass-per-recruit to half that of an unexploited stock ($F_{SB50}$) (Table 5.2). Spawner biomass-per-recruit decreased rapidly with increased fishing mortality to a level half of the unexploited levels, after which it was reduced slightly with large increases in $F$ (Fig. 5.4). This trend was similar with regard to the response of the yield-per-recruit curve to an increase in fishing mortality, increasing rapidly until $F = 0.4$ year$^{-1}$, after which there was only a marginal increase.

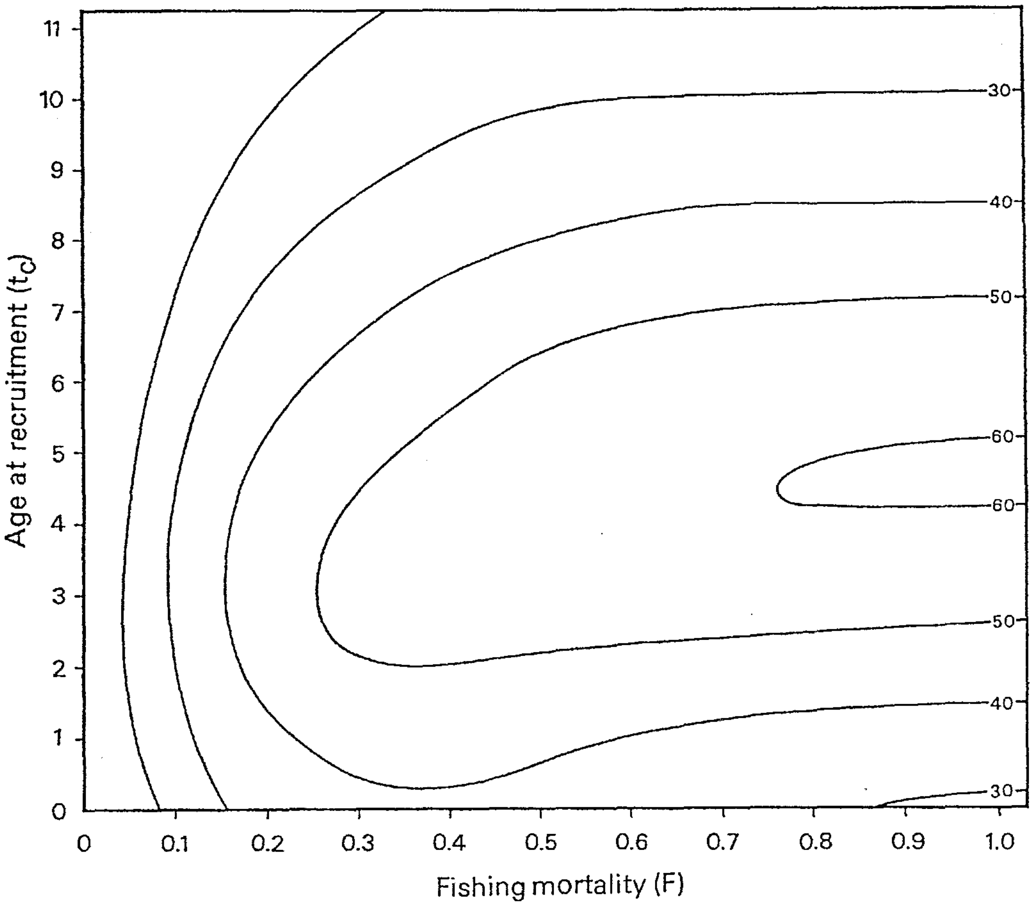

Fig. 5.2. Isopleth diagram describing the response of yield-per-recruit to different combinations of fishing mortality and age-at-50%-selectivity for *Pterogymnus laniarius* on the Agulhas Bank. Analysis was conducted using the "base case" scenario where $M = 0.28$ year$^{-1}$.

*Sensitivity analysis*

The results of the application of alternative input parameters to the yield-per-recruit and spawner biomass-per-recruit models is summarised in Table 5.3. Qualitatively, the results were similar to the "base case" analysis, in that a higher fishing pressure was necessary to maximise yield-per-recruit using the higher natural mortality scenario. A trend of increased effort for the different *TRPs* considered was evident when age-at-50%-selectivity was set after the age-at-maturation for both the natural mortality scenarios.

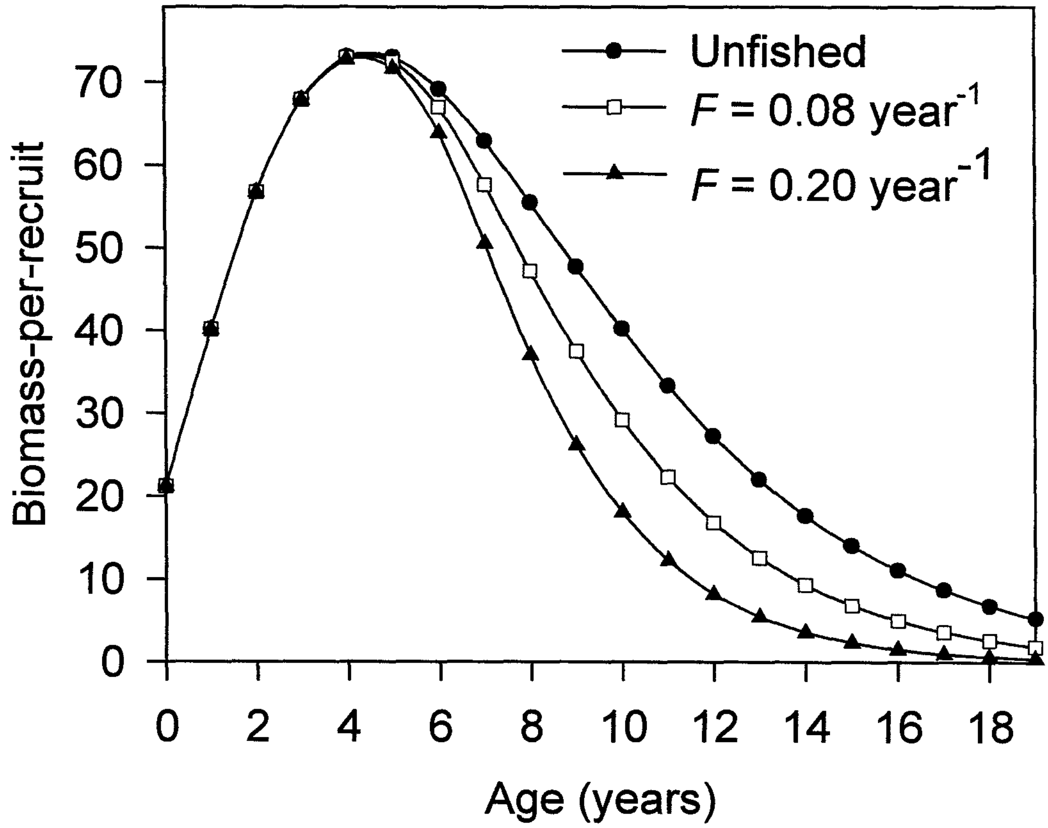

Fig. 5.3. Biomass-per-recruit as a function of age for *Pterogymnus laniarius* comparing an unfished population with two exploitation scenarios, one at current levels of $F$ = 0.08 year$^{-1}$ and $a_{50}$ = 5.5 years and at $F$ = 0.2 year$^{-1}$ and $a_{50}$ = 5.5 years. Analysis was conducted using the "base case" scenario where $M$ = 0.28 year$^{-1}$.

Table 5.2
The response of various target reference points and estimates of yield estimated using the Beverton and Holt yield-per-recruit model for *Pterogymnus laniarius* on the Agulhas Bank for the two "base case" scenarios. Yield values are given in metric tons per annum.

| | $F_{MAX}$ | $F_{0.1}$ | $F_{SB50}$ | $F_{SB40}$ | $Yield_{MAX}$ | $Yield_{0.1}$ | $Yield_{SB50}$ | $Yield_{SB40}$ |
|---|---|---|---|---|---|---|---|---|
| $M$ = 0.28 | ∞ | 0.39 | 0.30 | 0.48 | ∞ | 4302 | 3924 | 4555 |
| $M$ = 0.20 | ∞ | 0.25 | 0.18 | 0.27 | ∞ | 6443 | 5707 | 6579 |

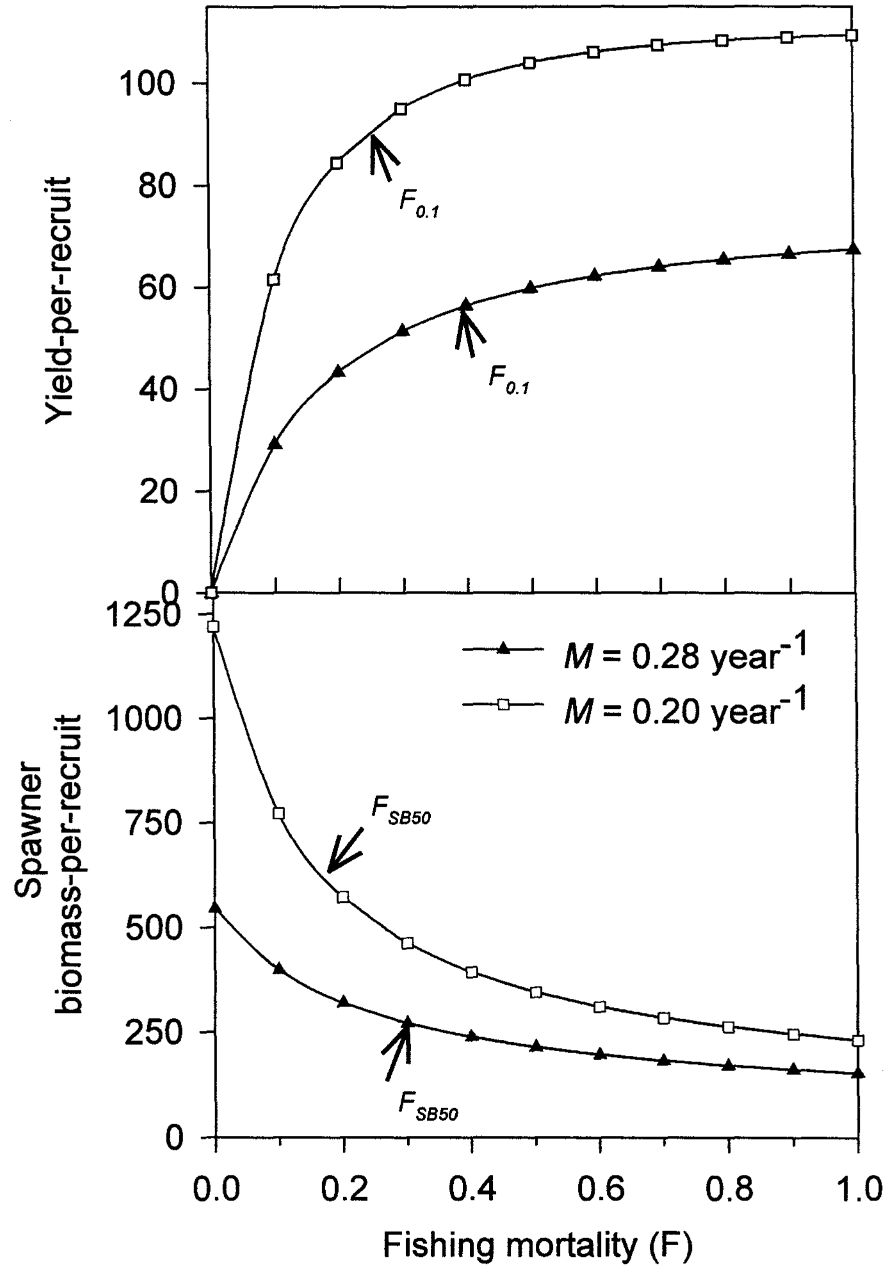

Fig. 5.4. Yield-per-recruit and spawner biomass-per-recruit as a function of fishing mortality (*F*) for *Pterogymnus laniarius* at two levels of natural mortality where $M$ = 0.28 year$^{-1}$ and 0.20 year$^{-1}$.

When age-at-maturity was attained before or at the age-at-50%-selectivity, the estimates for the various *TRPs* obtained from the spawner biomass-per-recruit curve were either greater or less than the "base case" scenario respectively (Table 5.3).

Table 5.3
The sensitivity of various target reference points and estimates of yield using the Beverton and Holt yield-per-recruit model for *Pterogymnus laniarius* on the Agulhas Bank to alternative input parameters. Note that knife-edged selectivity is approximated by setting $\delta$ = 0.01. Yield values are given in metric tons per annum.

| | $F_{MAX}$ | $F_{0.1}$ | $F_{SB50}$ | $F_{SB40}$ | $Yield_{MAX}$ | $Yield_{0.1}$ | $Yield_{SB50}$ | $Yield_{SB40}$ |
|---|---|---|---|---|---|---|---|---|
| $a_{50}$ = 7.3 years; $\delta$ = 0.9 year$^{-1}$ | | | | | | | | |
| $M$ = 0.28 | 6.15 | 0.48 | 0.62 | 1.21 | 5291 | 3775 | 4064 | 4657 |
| $M$ = 0.20 | ∞ | 0.30 | 0.29 | 0.52 | ∞ | 6443 | 5707 | 6579 |
| $a_{50}$ = 4 years; $\delta$ = 0.6 year$^{-1}$ | | | | | | | | |
| $M$ = 0.28 | ∞ | 0.32 | 0.18 | 0.26 | ∞ | 4571 | 3668 | 4271 |
| $M$ = 0.20 | ∞ | 0.21 | 0.12 | 0.18 | ∞ | 6414 | 5286 | 6098 |
| $a_{50}$ = 2.5 years; $\delta$ = 0.6 year$^{-1}$ | | | | | | | | |
| $M$ = 0.28 | ∞ | 0.25 | 0.12 | 0.17 | ∞ | 4478 | 3387 | 3945 |
| $M$ = 0.20 | ∞ | 0.17 | 0.09 | 0.13 | ∞ | 6025 | 4829 | 5557 |
| $\delta$ = 0.01 year$^{-1}$ | | | | | | | | |
| $M$ = 0.28 | ∞ | 0.39 | 0.32 | 0.57 | ∞ | 4280 | 4022 | 4706 |
| $M$ = 0.20 | ∞ | 0.26 | 0.18 | 0.29 | ∞ | 6526 | 5811 | 6727 |
| $t_m$ = 2.5 years | | | | | | | | |
| $M$ = 0.28 | ∞ | 0.39 | 0.45 | 0.87 | ∞ | 4302 | 4471 | 5097 |
| $M$ = 0.20 | ∞ | 0.25 | 0.22 | 0.37 | ∞ | 6443 | 6176 | 7037 |
| $t_m$ = 5.5 years | | | | | | | | |
| $M$ = 0.28 | ∞ | 0.39 | 0.20 | 0.29 | ∞ | 4302 | 3324 | 3914 |
| $M$ = 0.20 | ∞ | 0.25 | 0.14 | 0.20 | ∞ | 6443 | 5141 | 5993 |

## Discussion

The response of different per-recruit models to varying levels of fishing effort and recruitment for the panga stock was similar to those found for other reef fishes and sparids in general (Sato, 1980; Huntsman et al., 1983; Buxton, 1992; Smale and Punt, 1991; Pulfrich and Griffiths, 1988b; Punt et al., 1993). This is primarily a result of similarities in life-history patterns and age structure (Adams, 1980).

Theoretically, yield-per-recruit will peak if an infinite fishing mortality is applied at the moment the biomass of the cohort is at its maximum (Pereiro, 1992). If this maximum yield-per-recruit is maintained after the age-at-sexual maturity we can further reduce the risk of recruitment failure. Similarly, if age-at-maturity was less than, or equal to the age-at-50% selectivity, there could be an overfishing situation where the spawner biomass-per-recruit (or population growth potential - see Goodyear, 1993) would quickly reach a level where recruitment would fail. It is for this reason that the spawner biomass-per-recruit of the stock needs to be protected by preventing it from falling below a level at which it can replace itself. In most cases this is between 25 - 50% of unexploited levels (Clarke, 1991; Deriso, 1987; Sissenwine and Shepherd, 1987; Gabriel et al., 1989; Quinn et al., 1990; Punt, 1993b; Mace, 1994). Fortunately for panga, recruitment into the existing fisheries occurs at least 1.5 years after maturity, thus reducing the risk of recruitment overfishing. This is noticeable as there appears to be a marginal drop in spawner biomass per-recruit with large increases in fishing effort. In this case, despite increases in fishing pressure, the spawner biomass is protected by the selectivity of the gear which provides a spawner biomass "refuge". Sensitivity analysis also revealed that when age-at-50%-selection is greater than the age-at-50%-maturity, the stock appears to be more resilient and is able to sustain a higher fishing pressure. Although a scenario where fish are selected into the fishery after reaching sexual maturity suggests that there is no threat to the spawner biomass-per-recruit, the slow growth and longevity of this species needs to be monitored as it can result in possible growth overfishing.

In an attempt to define optimum fishing mortalities from a per-recruit perspective the use of target reference points has become common practice in fisheries management (Clarke, 1991; Punt, 1993b; Caddy and Mahon, 1995). Of the different *TRPs* chosen, deterministic simulations showed that a $F_{max}$ strategy consistently achieved the highest total catch at the expense of severe spawner biomass-per-recruit reduction (Punt, 1993b) . A $F_{SB35}$ strategy, though preferable to a $F_{max}$ strategy, also tended to fare poorly on occasions (from a resource conservation perspective) by reducing spawner biomass-per-recruit to less than 20% of unfished levels, despite Clarke's (1991) recommendations for its use for groundfish stocks. Punt (1993) concluded that a marginal yield strategy ($F_{0.1}$) was, on average, the most stable and could be used with relative safety with the least risk of stock collapse. Recently, Clark (1993) and Mace (1994) using stochastic models, confirmed these results and recommended that spawner biomass per-recruit should not be reduced below 40% of unfished levels, particularly where the stock-recruitment relationship is unknown. They also showed that $F_{0.1}$ estimates generally lie between the $F_{SB35}$ and $F_{SB40}$ reference points, particularly when recruitment and maturity schedules coincided.

From the results presented in this study, it appears that of the various *TRPs* investigated a $F_{SB50}$ strategy was the most suitable, and is probably adequate to protect the spawner stock in slow growing, long lived species (Buxton, 1992). Though this level is the most conservative of the *TRPs* investigated, the relationship between stock size and recruitment is presently unknown and any increase in effort must be considered with caution. The high estimates of $F_{SB40}$ were rejected as they were greater than the effort expended by the foreign fleet prior to the collapse of the stock (Sato, 1980). Another area of concern is that at levels of $F > 0.4$ $\text{year}^{-1}$ most of the spawner biomass-per-recruit would be reduced to one or two year classes. Maintaining such high fishing effort would be a risky strategy if there was a year class failure. This scenario, although possible, would possibly be quite rare as the panga is known to spawn throughout the year over the entire Agulhas Bank (Chapter 3).

Current panga fishing mortality estimates were found to be considerably lower than the predicted marginal yield values. This would suggest that the panga stock can sustain a higher fishing pressure than is the case at the moment. Though the stock appears to be in a "healthy situation" it is difficult to predict an optimal catch without prior knowledge of the stock-recruitment relationship. Preliminary estimates suggest that an optimum catch in the range of 3900 - 5700 *t* per annum, representing a 5-7 fold increase in panga catches of the South African fishing fleet. This range incorporates the predicted optimal catch proposed by Sato (1980) of 5000 *t*. It must be noted, however, that Sato's (1980) results should be viewed with caution as no spawner biomass-per-recruit analysis was conducted, which would have possibly suggested the unsustainability of the proposed catch levels. This is confirmed by the results of the sensitivity analysis using $a_{50}$ = 2.5 years, with estimates of $F_{SB50}$ and $F_{SB40}$ at which the predicted yield would have been lower than those for a $F_{0.1}$ strategy, which was the *TRP* chosen in the previous analysis.

Problems arise whilst managing a single species within the different multispecies and multiuser fisheries that harvest it. To facilitate management, two commonly used regulatory mechanisms are size and effort restrictions. In the South African trawlfisheries, the present regulatory minimum mesh size (75 mm stretched mesh cod-end) reduces the capture of small fish, particularly in vessels directing effort towards hake and horse mackerel. In contrast, in the offshore linefishery, there are no size restrictions imposed on fishers catching panga. The capture of small fish is, however, reduced due to market forces. In most ports, panga are landed at a relatively large size with the exception of ports on the Western Agulhas Bank, where fish tend both to be smaller (Badenhorst and Smale, 1991) and acceptable in the market. Fortunately, panga landings from ports on the Western Agulhas Bank are small due to the low abundance and insignificant in relation to the total landed catch. In the future, these conditions will hopefully continue to provide a mechanism for maintaining selectivity at its present age as this species is subject to extreme barotrauma as a result of its capture from depths in excess of 60 m, which substantially reduces survival of fish returned to the sea. Fishing effort is more difficult to estimate and regulate as this species is predominantly an incidental bycatch in the various multispecies fishing sectors. A thorough knowledge of the relative fishing pressures and gear selectivities of the different fishing sectors is, therefore, necessary before a comprehensive estimate of effort can be made.

In an attempt to overcome our uncertainty, the use of per-recruit analysis for management advice implies an assumption of knowledge of the mechanisms that define the biological behaviour of a stock in response to its exploitation as well as the accurate parameterisation of growth, maturity, mortality and selectivity patterns. Although per-recruit analysis has limitations *inter alia* nonstationarity in the parameter estimates, the lack of a stock-recruitment relationship and the difficulty is translating fishing mortality to fishing effort (Norris, 1991; Pereiro, 1992), it is these limitations that point to its use as a suitable management tool for predictions in the short rather than in the long term. These results must, therefore, be combined with other age-structured models in order to provide a more accurate, comprehensive and sustainable strategy for the management of the panga stock on the Agulhas Bank.

# Chapter 6 - Stock assessment of the panga using an age-structured production model

## Introduction

Previous assessments of the panga stock using surplus-production (Sato, 1980) and per-recruit models (Chapter 5), have both suggested that catches some five to seven times higher than present levels may be sustainable. The large reduction in fishing effort directed towards panga over the past 18 years has also led to some speculation within the fishing industry that this resource may have recovered and could support larger catches in the future. In this chapter, an alternative assessment of the panga resource is presented, using a deterministic age-structured production model to ascertain whether the panga resource on the Agulhas Bank has recovered to a state that it can support increased catches.

## Materials and Methods

### *Estimation framework*

Assessment of the panga resource is complicated by the complex multi-user nature of the fishery (Chapter 1). Since annual age-composition data are not available, stock assessment methods which require these data such as *ad hoc* tuned Virtual Population Analysis (Pope and Shepherd, 1985; Butterworth et al., 1990) and integrated analysis (Deriso et al., 1985) cannot be applied.

The only data available for assessment purposes are the time-series of annual catches from 1895 - 1995 (Fig. 6.1) and the results from fishery-independent surveys of the Agulhas Bank from 1988-1995 (Table 6.1).

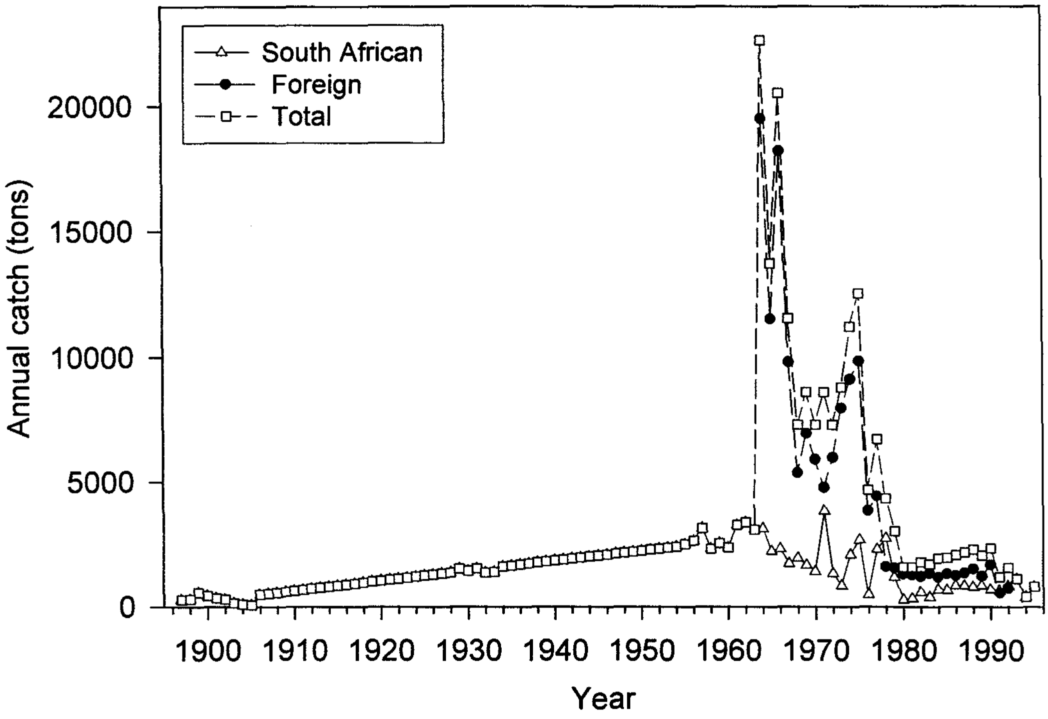

Fig. 6.1. Catch history (1895 - 1995) of *Pterogymnus laniarius* on the Agulhas Bank.

No attempt was made to standardise the commercial catches with respect to changes in fishing practices over time. The unstandardised catch data would, however, not significantly effect the analysis, as this data series was used to calculate annual age-structure with the estimation framework. Details regarding the sources of the catch data from the South African and foreign fleets used in the analysis are summarised in Table 2.1. The survey methodology is outlined in detail in Chapters 2 and 4. Catch rate information was available from 1984 for the inshore trawl component of the fishery, but these data (Table 6.2) are of questionable value owing to the multispecies nature of the fishery. A further concern with this data is that it has yet to be standardised to remove the effects of changes in fishing practices over time. For this reason, the catch rate information was not used directly in the analyses.

Table 6.1
Estimates of *Pterogymnus laniarius* abundance with associated coefficients of variation (in parenthesis) determined from random stratified surveys conducted between 1988 and 1996. For those years in which two surveys took place, the inverse variance weighted average of the two estimates is presented. The statistic *SLOPE* is the annual percentage change in abundance, calculated as a ratio of the slope of a linear regression through the points divided by the mean biomass estimate over the time period, multiplied by 100. The figures in parenthesis next to the value of the slope of the regression are the *p-values* for the slopes. Estimates of biomass are given in thousand metric tons.

| Year | Autumn/Winter surveys | | | Spring/Summer surveys | | | Averaged |
|---|---|---|---|---|---|---|---|
| | Month | #trawl | Estimate | Month | #trawl | Estimate | Estimate |
| 1988 | May | 93 | 49.84 (20.1) | - | - | - | 49.84 (20.1) |
| 1989 | May | 62 | 58.85 (25.4) | - | - | - | 58.85 (25.4) |
| 1990 | May | 58 | 55.82 (29.5) | Sept. | 73 | 66.09 (21.7) | 61.66 (17.5) |
| 1991 | June | 91 | 88.60 (34.9) | Sept. | 75 | 92.69 (16.5) | 91.89 (14.9) |
| 1992 | Mar. | 82 | 56.11 (17.3) | Sept. | 87 | 93.95 (12.8) | 71.08 (10.6) |
| 1993 | Apr. | 109 | 89.96 (12.6) | Sept. | 104 | 70.54 (14.8) | 79.41 (9.7) |
| 1994 | June | 88 | 67.37 (15.9) | Sept. | 92 | 86.72 (17.0) | 74.04 (11.7) |
| 1995 | Apr. | 92 | 99.04 (14.9) | Sept. | 96 | 74.33 (14.0) | 82.53 (10.3) |
| 1996* | Apr. | 77 | 88.44 (21.7) | - | - | - | 88.44 (21.7) |
| *SLOPE* | | | 6.9 (0.025) | | | 0.0 (0.998) | 5.3 (0.016) |

*Ignored for the purposes of the analyses of this study

The lack of age-composition data within the catches means that the assessment has to be based on some form of surplus-production model. The most commonly used estimation procedures (e.g. Schaefer, 1954, 1957; Butterworth and Andrew, 1984) ignore age-structure effects and instead treat the biomass as a lumped variable. Most biologists and fisheries managers are now more comfortable with models which explicitly account for age-structure. Furthermore, lumped biomass models can only be used to evaluate a limited number of management options. A form of production model which takes age-structure effects into account but does not require information about the age-composition of the catches is an age-structured production model (e.g. Hilborn, 1990; Francis, 1992; Punt, 1994; Punt and Japp, 1994). This is, therefore, the most suitable approach to evaluate the status and productivity of the panga resource.

The panga resource on the Agulhas Bank is assumed to be a single stock because more than 90% of juvenile panga utilise a large nursery area on the Central Agulhas Bank (Chapter 4). Although panga are found from the west to the east coast of South Africa, few panga are found east of East London and west of Cape Agulhas. In fact, more than 95% of the catch of panga is taken between Cape Agulhas and East London.

Table 6.2
Catch rate data for *Pterogymnus laniarius* from the inshore trawl fleet (1984 - 1995). Catch rate estimates were obtained by dividing the annual undirected catches by the total effort of the entire hake directed inshore trawl fleet operating on the South coast. The statistic SLOPE is defined in Table 6.1

| Year | Effort (Thousand trawler days) | Catch rate (Metric tons . thousand trawler days$^{-1}$) |
|---|---|---|
| 1984 | 78.4 | 7.9 |
| 1985 | 83.9 | 6.7 |
| 1986 | 81.2 | 6.4 |
| 1987 | 76.0 | 8.3 |
| 1988 | 83.2 | 6.6 |
| 1989 | 101.5 | 5.4 |
| 1990 | 97.1 | 3.4 |
| 1991 | 89.5 | 4.4 |
| 1992 | 75.8 | 5.9 |
| 1993 | 58.6 | 12.6 |
| 1994 | 62.5 | 7.1 |
| 1995 | 70.5 | 7.5 |
| SLOPE | -1.9% | 1.1% |

The estimates of the model parameters and hence of any management-related quantities were obtained by maximising a likelihood function, which contains a contribution related to the fit to the survey indices of abundance. The underlying age-structured production model and the likelihood function considered are described below.

Resource dynamics

The dynamics of fish aged 1 year and older are governed by:

$$N_{y+1,a} = \begin{cases} R_{y+1} & \text{if } a = 0 \\ N_{y,a-1}\, e^{-Z_{y,a-1}} & \text{if } 1 \le a < x \\ N_{y,x-1}\, e^{-Z_{y,x-1}} + N_{y,x}\, e^{-Z_{y,x}} & \text{if } a = x \end{cases} \qquad \text{(Equation 6.1)}$$

where $N_{y,a}$ is the number of fish of age $a$ at the start of the year $y$, $R_y$ is the number of 0-year-olds at the start of year $y$, $x$ is the maximum age (taken to be a plus-group), $Z_{y,a}$ is the total mortality on fish of age $a$ during year $y$, with

$$Z_{y,a} = M + S_a^{SA}\, F_y^{SA} + S_a^{FO}\, F_y^{FO} \qquad \text{(Equation.6.2)}$$

where $M$ is the instantaneous rate of natural mortality (assumed to be independent of age and time), $S_a^{SA}$ and $S_a^{FO}$ are the age-specific selectivity functions for the South African and foreign (Japanese and Taiwanese) trawlfisheries respectively, and $F_y^{SA}$ and $F_y^{FO}$ are the fully-selected fishing mortalities during year $y$ for these fisheries.

Recruitment

This is governed by the deterministic Beverton and Holt stock-recruitment relationship which has been shown to be suitable for this form of analysis (Punt, 1994; Punt et al., 1995). The number of recruits during year $y$, $R_y$, is calculated as:

$$R_y = \frac{SB_y}{\alpha + \beta SB_y} \qquad \text{(Equation 6.3)}$$

where $SB_y$ is the spawning biomass at the start of year $y$, and is calculated as:

$$SB_y = \sum_{a=a_m}^{x} w_a \, N_{y,a} \qquad \text{(Equation 6.4)}$$

where $w_a$ is the mass of a fish of age $a$ at the start of the year:

$$\begin{aligned} w_a &= e(L_a)^f \\ L_a &= L_\infty(1-e^{-\kappa(a-t_0)}) \end{aligned} \qquad \text{(Equation 6.5)}$$

$a_m$ is the age-at-maturity, $L_\infty$, $\kappa$ and $t_0$ are the von Bertalanffy growth equation parameters, and $e$ and $f$ are the mass-length relationship parameters.

Catches

The fully-selected fishing mortalities $F_y^{SA}$ and $F_y^{FO}$ are calculated by solving the following coupled equations:

$$\begin{aligned} C_y^{SA} &= \sum_{a=0}^{x} w_{a+1/2} \, S_a^{SA} \, F_y^{SA} \, N_{y,a}[1-e^{-Z_{y,a}}]/Z_{y,a} \\ C_y^{FO} &= \sum_{a=0}^{x} w_{a+1/2} \, S_a^{FO} \, F_y^{FO} \, N_{y,a}[1-e^{-Z_{y,a}}]/Z_{y,a} \end{aligned} \qquad \text{(Equation 6.6)}$$

where $C_y^{SA}$ and $C_y^{FO}$ are the South African and foreign catches (by mass) in year $y$, and $w_{a+1/2}$ is the mass of a fish of age $a$ in the middle of the year. The solution of Equation (6.6) was achieved using an iterative linear bisection technique.

Age-specific selectivity

The selectivity pattern for both the South African and foreign trawl fleets is assumed to be time invariant and to have the logistic form:

$$S_a = \frac{1}{1+e^{-(a-a_{50})/\delta}} \qquad \text{(Equation 6.7)}$$

where $S_a$ is the selectivity of the gear on a fish of age $a$, $a_{50}$ is the age-at-50%-selectivity, and $\delta$ is the parameter which determines the width of the age-specific selectivity function. Note that because the relative contributions by the South African and the foreign fleets to the total catch vary over time, the overall selectivity pattern is not time-invariant.

Initial conditions

The resource is assumed to have been at its unexploited equilibrium level at the start of 1898 (despite some relatively small catches before this; Fig. 6.1) with an age structure determined by the formula $N_{1898,a} = R_0 n_a$ where:

$$n_a = \begin{cases} 1 & \text{if } a = 0 \\ \exp(-a\,M) & \text{if } 1 \le a < x \\ \exp(-x\,M)/(1-\exp(-M)) & \text{if } a = x \end{cases} \qquad \text{(Equation 6.8)}$$

where $R_0$ is the number of 0-year-olds at the deterministic equilibrium that corresponds to an absence of harvesting. $R_0$ is calculated from the value for $K^T$ (the total biomass of the resource in the absence of harvesting):

$$R_0 = K^T / \sum_{a=0}^{x} w_a\, n_a \qquad \text{(Equation 6.9)}$$

The values for the stock-recruitment relationship parameters $\alpha$ and $\beta$ are calculated from $R_0$ and the “steepness” of the stock-recruitment relationship, $h$. “Steepness” is defined as the fraction of the number of recruits at unexploited equilibrium expected when the spawning biomass is reduced to 20% of its pristine level (Francis, 1992), so that:

$$\alpha = \frac{(1-h)}{4h} \sum_{a=a_m}^{x} w_a\, n_a$$
$$\beta = \frac{5h-1}{4h R_0} \qquad \text{(Equation 6.10)}$$

Yield estimation

An estimate of yield is obtained from the sustainable yield *vs* fishing mortality curve:

$$C(F) = YPR(F)\,R(F) \qquad \text{(Equation 6.11)}$$

where *C*(*F*) is the equilibrium catch corresponding to a fully-selected fishing mortality of *F*, *YPR*(*F*) is the yield-per-recruit function, and *R*(*F*) is recruitment as a function of fishing mortality.

The yield-per-recruit *vs F* relationship given by Butterworth et al. (1990) is:

$$YPR(F) = \sum_{a=0}^{x} w_{a+1/2}\, S_a\, F\, \widetilde{N}_a [1 - e^{-(M+S_a F)}] / (M + S_a F) \qquad \text{(Equation 6.12)}$$

where

$$\widetilde{N}_a = \begin{cases} 1 & \text{if } a = 0 \\ \widetilde{N}_{a-1}\, e^{-(M+S_{a-1}F)} & \text{if } 1 \le a < x \\ \widetilde{N}_{x-1}\, e^{-(M+S_{x-1}F)} / (1 - e^{-(M+S_x F)}) & \text{if } a = x \end{cases} \qquad \text{(Equation 6.13)}$$

The equilibrium recruitment corresponding to a fishing mortality of *F* is:

$$R(F) = \tfrac{1}{\beta}(1 - \alpha / \widetilde{S}(F)) \qquad \text{(Equation 6.14)}$$

where $\widetilde{S}(F)$ is spawner-biomass-per-recruit as a function of *F*:

$$\widetilde{S}(F) = \sum_{a=a_m}^{x} w_a\, \widetilde{N}_a \qquad \text{(Equation 6.15)}$$

Maximum likelihood function

The two series of biomass estimates (spring and autumn) are assumed to be indices of relative abundance. Each survey estimate is assumed to be log-normally distributed about its expected value, i.e.:

$$O_j^i = q^i E_j^i e^{\varepsilon_j^i} \qquad \varepsilon_j^i \sim N[0;(\sigma^i)^2] \qquad \text{(Equation 6.15)}$$

where $O_j^i$ is the actual biomass estimate for year $j$ and series $i$, $q^i$ is the constant of proportionality for series $i$, and $E_j^i$ is the model estimate corresponding to $O_j^i$:

$$E_j^i = \sum_{a=1}^{x} w_{a+1/2} N_{y,a} e^{-Z_{y,a}/2} \qquad \text{(Equation 6.16)}$$

The contribution of abundance series $i$ to the likelihood function is therefore:

$$L^i = \prod_j \frac{1}{O_j^i \sqrt{2\pi}\,\sigma^i} e^{-\left(\frac{(\ell n O_j^i - \ell n(q^i E_j^i))^2}{2(\sigma^i)^2}\right)} \qquad \text{(Equation 6.17)}$$

where the summation is over the years for which abundance estimates are available for series $i$.

Maximum likelihood estimates for $q^i$ and $\sigma^i$ can be obtained by differentiating Equation 6.17 with respect to the parameter of interest and solving the resulting equation, i.e.:

$$\hat{q}^i = \exp\left(\tfrac{1}{n^i}\sum_y \ell n(O_j^i / E_j^i)\right)$$
$$\hat{\sigma}^i = \sqrt{\tfrac{1}{n^i}\sum_y \ell n(\hat{q}^i E_j^i / O_j^i)^2} \qquad \text{(Equation 6.18)}$$

where $n^i$ is the number of data points for biomass series $i$.

Substituting the maximum likelihood estimates of $q^i$ and $\sigma^i$ into Equation 6.17 , taking logarithms, negating, and dropping the terms independent of the model parameters gives the quantity minimised to find the maximum likelihood estimates for $R_0$ and $h$:

$$-\ell nL = \sum_i \left( n^i \ell n \hat{\sigma}^i + n^i / 2 \right) \qquad \text{(Equation 6.19)}$$

*Values for model parameters*

Values for only two of the parameters of the population dynamics model (steepness and virgin biomass - see Equations 6.9 and 6.10) are estimated by maximising the likelihood function. The values for the other parameters are set using results from previous studies (Table 6.3).

As is the case for most other marine fishes, estimation of the instantaneous rate of natural mortality, *M*, for panga has proved problematic. Estimates of *M* from the empirical methods of Pauly (1980) and Rikhter and Efanov (1977), 0.16 $\text{yr}^{-1}$ and 0.41 $\text{yr}^{-1}$, respectively, seem unrealistic as they were either considerably lower or higher then *Z*. Both estimates were averaged to obtain a first approximation to *M* of 0.28$\text{yr}^{-1}$ (Chapter 3). This estimate, along with Sato's (1980) estimate of 0.2 $\text{yr}^{-1}$, was used in further analyses.

The plus-group was set at age 20 in this study. Although 16 years was the maximum age recorded and age of 20 years is likely. This is because the ageing of large fish was problematic due to the heavily calcified nature of the otoliths (Chapter 3). Fortunately, this specification has very little impact on the final estimations.

The "base case" choices for the values of the selectivity parameters were determined using age composition data from the inshore trawlfishery catches between 1994 and 1996. Fish were first caught at 4 years of age and were fully recruited by 7 years, with the age-at-50%-selectivity estimated at 5.5 years. The estimation of $a_{50}$ and $\delta$ (see Table 6.3) was based on the assumptions that the modal age in the catch (age 7) corresponds to that at which selectivity is 0.975, while at age 4 selectivity is 0.025. The values for the parameters of the age-specific selectivity pattern for the foreign trawlfishery were obtained from the results of covered cod-end selectivity experiments (Sato, 1980).

Table 6.3
"Base case" values for the fixed parameters of the population dynamics model and the values considered in the tests of sensitivity (in parenthesis).

| Parameter | Estimate | Source |
|---|---|---|
| $L_\infty$ (mm) | 379.4 | Chapter 3 |
| $\kappa$ (yr$^{-1}$) | 0.13 | Chapter 3 |
| $t_0$ (years) | -1.78 | Chapter 3 |
| $e$ (g.mm$^{-1}$) | 0.00002 | Chapter 3 |
| $F$ | 3.031 | Chapter 3 |
| $M$ (yr$^{-1}$) | 0.2; 0.28 | See text |
| $x$ (years) | 20 | See text |
| $a_m$ (years) | 4 (3, 5) | Chapter 3 |
| $a_{50}^{SA}$ (years) | 5.5 (2.7, 4) | See text |
| $a_{50}^{FO}$ (years) | 2.7 | Selectivity-at-age was obtained directly from Sato (1980) without the quantity $\delta^{FO}$ being specified |
| $\delta^{SA}$ (years) | 0.4 (knife-edged) | See text |
| Trawl selectivity in biomass series | Ignored (incorporated) | See text |

The surveys upon which the abundance estimates in Table 6.1 are based are essentially non-selective as cod-end net liners were used to capture small fish. However, it was also clear that these surveys do not index the total population size because trawling rarely occurred on the nursery grounds on the Central Agulhas Bank. The "base case" assumption of this study was, therefore, that these surveys are indices of the biomass of all animals aged 1 and above. The sensitivity of the results to the alternative specification that the selectivity pattern for the surveys was the same as that for the trawlfishery is also explored.

*Sensitivity tests*

The sensitivity tests involve changes to the biomass survey data, the age-at-maturity, the age-at-50%-selectivity and the width of the selectivity ogives. The tests of sensitivity which involve changes to the values for some of the fixed parameters of the model are detailed in Table 6.3.

*Management-related quantities*

The 15 management-related quantities used to assess the status and productivity of the stock are:

$K^s$ - spawning biomass at unexploited equilibrium,

$SB_{95}$ - spawning biomass at the start of 1995,

$SB_{95}/K^s$ - current depletion in 1995,

$SB_{95}/SB_{77}$ - ratio of the spawning biomass at the start of 1995 to that at the start of 1977,

$SB_{95}/SB_{MSY}$ - ratio of the spawning biomass at the start of 1995 to that at which $MSY$ occurs,

$SLOPE$ - slope of a linear regression of the biomass which corresponds to the survey indices of abundance over the period 1988 - 1995, divided by the estimate for 1992, and expressed as a percentage.

$C_{MSY}$ - Maximum Sustainable Yield (see Equations 6.11 - 6.15),

$F_{MSY}$ - fully-selected fishing mortality at which $MSY$ occurs,

$MSYR$ - ratio of $MSY$ to the spawning biomass at which it occurs (i.e. $C_{\mathrm{MSY}} / SB_{\mathrm{MSY}}$),

$C_{0.1}$ - catch at which the slope of the yield vs $F$ curve (Equation 6.11) is 10% of that at the origin,

$F_{0.1}$ - fully-selected fishing mortality at which $C_{0.1}$ occurs,

$0.1R$ - ratio of $C_{0.1}$ to the spawning biomass at which it occurs (i.e. $C_{0.1}/SB_{0.1}$),

$C_{SB50}$ - equilibrium catch at which the spawning biomass is half that of the pristine level,

$F_{SB50}$ - fully-selected fishing mortality at which $C_{SB50}$ occurs,

$-lnL$ - negative of the logarithm of the likelihood function (see Equation 6.19).

The first three of these quantities are related to the status of the panga resource relative to its pristine level. The next three statistics estimate the extent of recovery in the stock whilst $C_{MSY}$, $F_{MSY}$, $MSYR$, $C_{0.1}$, $F_{0.1}$, $0.1R$, $C_{SB50}$ and $F_{SB50}$ describe the potential yield of a trawl-based fishery. The negative log-likelihood ($-lnL$) and the *SLOPE* statistic are used to assess how well the model fits the data.

### Variance estimation

Coefficients of variation for the management-related quantities were estimated using the (conditioned) parametric bootstrap method (Efron, 1982; Punt, 1994; Punt and Butterworth, 1993) with 200 replicates. This is detailed in Equations 4.9 - 4.11. Confidence intervals were determined using the percentile method (Buckland, 1984).

## Results

### Biomass estimates

The biomass indices, their coefficients of variation and the measures of annual change in the biomass available to the survey gear are given in Table 6.1. While the autumn/winter biomass series increases at 6.8% p.a., the spring/summer biomass series was temporally uncorrelated. Combining both series results in a similar rate of increase to that of the inverse variance weighted average of the two series (5.3% p.a.). On average, the biomass indices for autumn/winter are less than those for spring/summer.

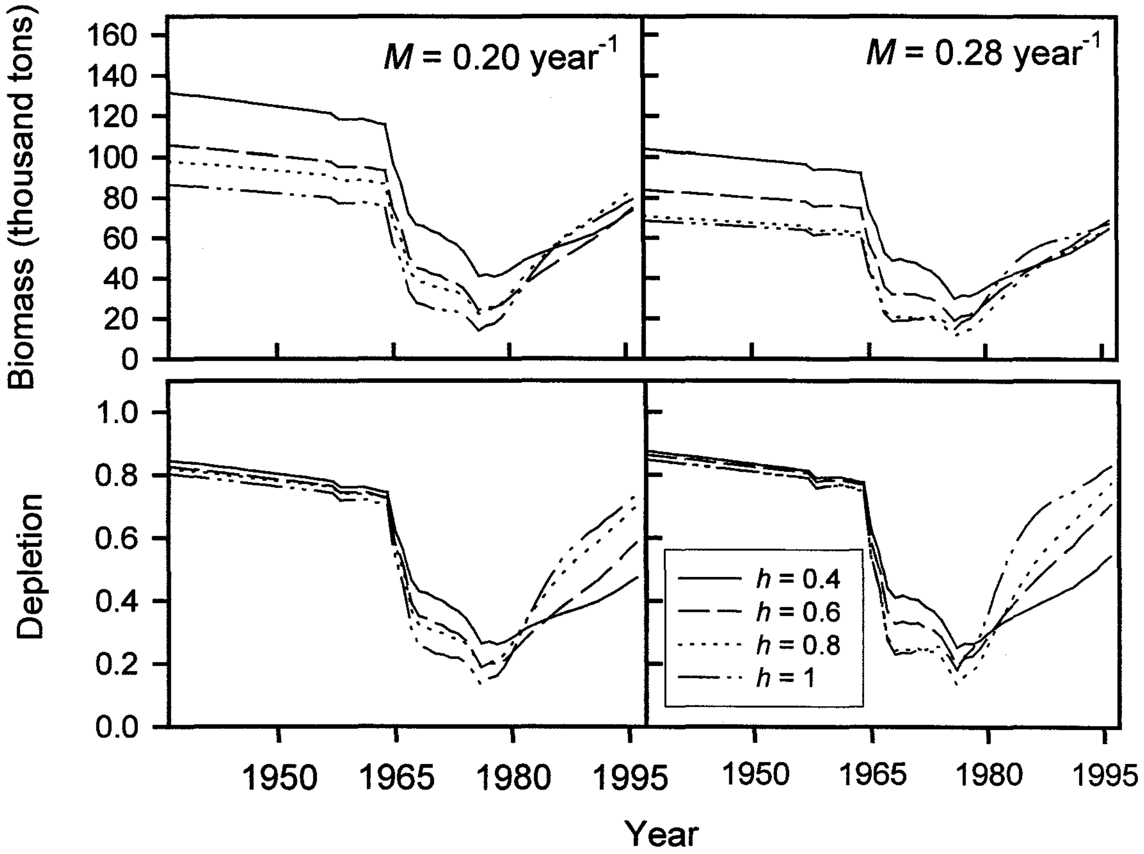

Fig. 6.2. Time-trajectories of spawning biomass for the *Pterogymnus laniarius* stock on the Agulhas Bank for four choices for the "steepness" parameter $h$. Results are shown for $M$ = 0.20 yr$^{-1}$ and $M$ = 0.28 yr$^{-1}$. The remaining parameters are set to their "base case" values. The upper panels show the spawning biomass in absolute terms and the lower panels show the spawning biomass as a fraction of its pristine level ("depletion").

### *Production modelling - "base case" analyses*

Point estimates for the 15 management-related quantities are given in Table 6.4 for a range of fixed values for the steepness parameter, $h$. The range considered (0.2 - 1) covers the entire spectrum of possibilities from no compensation ($h$ = 0.2) to no reduction in recruitment even if the spawner biomass drops to a very low level ($h$ = 1).

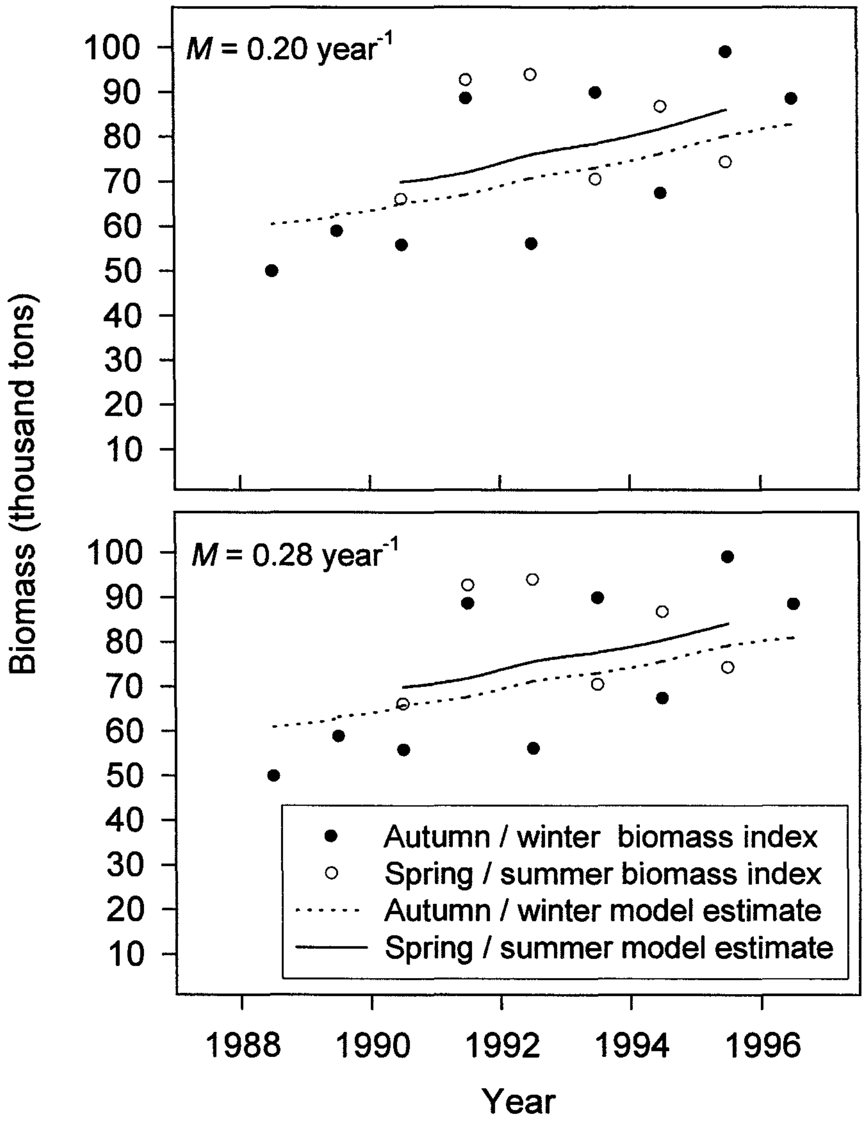

Fig. 6.3. Observed survey indices of abundance and the corresponding model estimates. Results are shown for the two choices for *M*. The estimates of biomass from the model have been scaled by their catchability coefficients to place them on the same scale as the biomass indices.

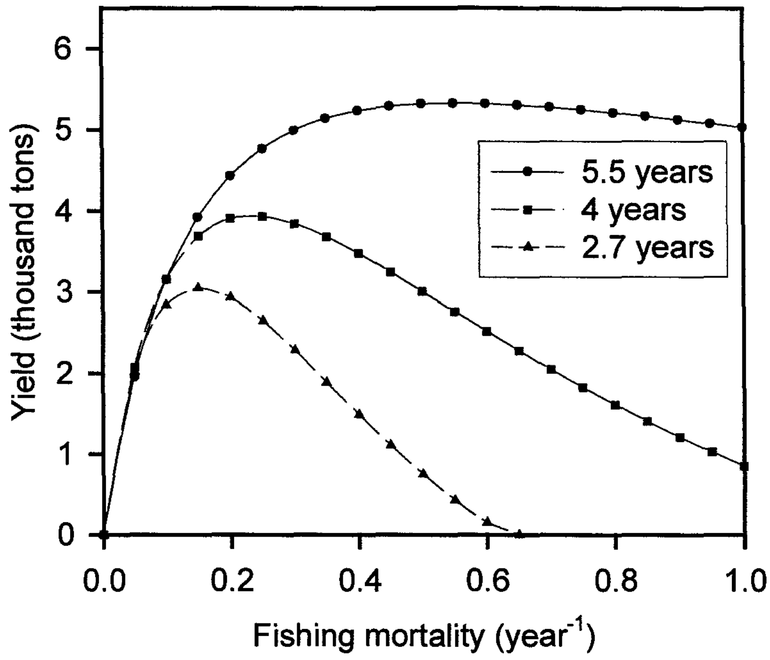

Fig. 6.4. Relationship between yield and fishing mortality for three alternative specifications of the age-at-50%-selectivity.

Not surprisingly, the results are strongly dependent on the value assumed for steepness. The stock is estimated to be less depleted and to have a higher sustainable yield for higher values for this parameter. Quantities such as current biomass and *MSY* are much less sensitive to the value for $h$ (for $h > 0.2$) than others, such as $F_{MSY}$ and $K^s$. The data are relatively uninformative about the "steepness" of the stock-recruitment relationship. Only the fits corresponding to the lowest value considered for $h$ are poorer than those corresponding to the maximum likelihood estimates for this parameter ($h = 0.65$ for $M = 0.2$ yr$^{-1}$; $h = 0.59$ for $M = 0.28$ yr$^{-1}$).

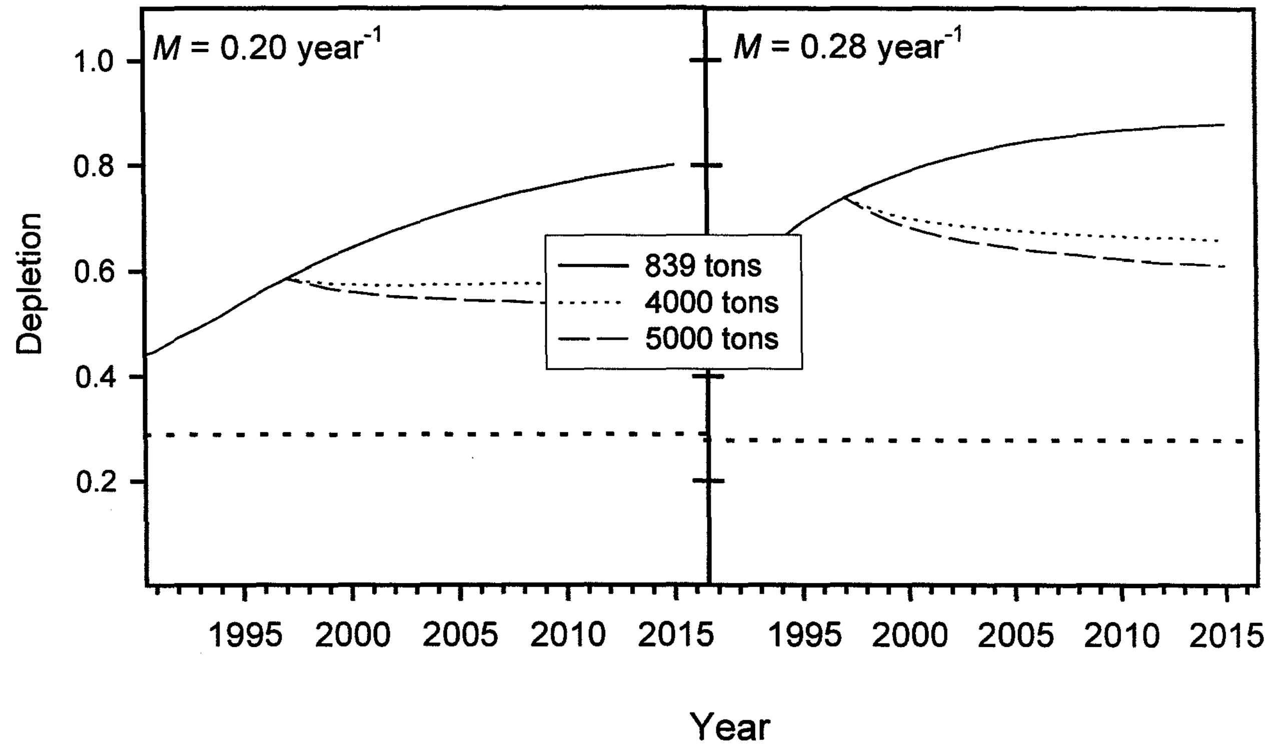

Fig. 6.5. Projections of spawning biomass as a fraction of its pristine level ("depletion") over the twenty-five year period 1990 to 2015. Results are based on the point estimates for the two "base case" analyses for three scenarios regarding future catches: the arithmetic mean of South African catches between 1980 and 1995 of 839*t*, and catches of 4000 and 5000*t*. The horizontal dotted line represents the depletion level where $C_{MSY}$ is attained.

Figure 6.2 shows the time-trajectories of spawning biomass for a variety of choices for the steepness parameter. The results are expressed in both absolute terms and as a fraction of the unexploited equilibrium level. For values of steepness of 0.4 and above, the results indicate a rapid decline in spawner biomass in the mid-1960's with the biomass dropping to some 20% of pristine levels between 1976 and 1977. As a consequence of the dramatic reduction in directed effort towards panga from 1978 onwards, the spawning biomass was estimated to have increased with the extent of increase being strongly dependent on steepness (Table 6.4; Figure 6.2). For values of steepness of 0.4 and above, the spawner biomass was estimated to be above that at which *MSY* is achieved, and to be well above the spawning biomass in 1977.

The consequences for $h = 0.2$ are more pessimistic, with fits to the data being relatively poor compared to the fits for other values of $h$ (Table 6.4). Furthermore, estimates of $h < 0.3$ based on fits to time-series of spawner stock and recruitment data are very uncommon for demersal fish species (J. Ianelli, NMFS, NOAA, pers. comm.).

The results are sensitive to the value assumed for $M$. The estimates of spawning biomass and sustainable yield for $M = 0.28$ yr$^{-1}$ are lower than those for $M = 0.2$yr$^{-1}$ for comparable values for $h$. However, when the spawning biomass is expressed as a fraction of the unexploited equilibrium level, the spawning biomass in 1977, or the spawning biomass at which *MSY* is achieved, the results for $M = 0.28$ yr$^{-1}$ are more optimistic. The results for $M = 0.28$ yr$^{-1}$ indicate higher values for *MSYR* for comparable values of $h$ than those for $M = 0.2$ yr$^{-1}$. This occurs because of yield-per-recruit effects.

Table 6.5 presents point estimates and bootstrap results for the two choices of $M$. Results are shown in Table 6.5 for two scenarios related to steepness where steepness is estimated and where steepness is assumed to be known exactly ($h = 0.65$ for $M = 0.2$ yr$^{-1}$ and $h = 0.59$ for $M = 0.28$ yr$^{-1}$). The fits to the biomass indices are shown in Figure 6.3. Although there is considerable unexplained variability about the fitted curves in Figure 6.3, there is no evidence for model mis-specification. For both choices of $M$, the data are uninformative about steepness, with the 95% confidence intervals for $h$ including most of the range of possible values. The parameters are fairly poorly determined compared with those for other South African demersal fish species (e.g. Punt, 1994; Punt and Japp, 1994). Nevertheless, the conclusion that the panga resource has recovered to some extent is indicated with considerable certainty because the probability that the spawning biomass in 1995 was greater than that in 1977 is at least 0.83 for both natural mortality scenarios considered.

Table 6.4

Estimates of 15 management-related quantities for "base case" application of the estimation procedure. Results are shown for five choices of the steepness parameter $h$ and the two choices for natural mortality, $M$.

(a) $M = 0.20$ yr$^{-1}$

| Quantity | $h$ = 0.2* | $h$ = 0.4 | $h$ = 0.6 | $h$ = 0.8 | $h$ = 1.0 |
|---|---|---|---|---|---|
| $K^s$ (x$10^3$ $t$) | 251.0 | 161.4 | 131.5 | 113.4 | 105.2 |
| $SB_{95}$ (x$10^3$ $t$) | 66.8 | 80.6 | 77.9 | 76.0 | 74.5 |
| $SB_{95}/K^s$ | 0.28 | 0.50 | 0.59 | 0.67 | 0.71 |
| $SB_{95}$ / $SB_{77}$ | 0.79 | 1.66 | 2.59 | 5.36 | 4.68 |
| $SB_{95}$ / $SB_{MSY}$ | 0.37 | 1.56 | 2.16 | 2.53 | 3.31 |
| $F_{MSY}$ | 0.00 | 0.12 | 0.26 | 0.46 | 0.75 |
| $C_{MSY}$ (x $10^3$ $t$) | 0.00 | 4.24 | 5.42 | 5.66 | 6.46 |
| $MSYR$ (%) | 0.00 | 8.24 | 15.07 | 21.68 | 27.73 |
| $F_{0.1}$ | 0.00 | 0.09 | 0.16 | 0.21 | 0.24 |
| $C_{0.1}$ (x $10^3$ $t$) | 0.00 | 4.13 | 5.14 | 5.45 | 5.61 |
| $0.1R$ (%) | 0.00 | 6.41 | 10.43 | 12.89 | 14.23 |
| $F_{SB50}$ | 0.00 | 0.07 | 0.10 | 0.13 | 0.15 |
| $C_{SB50}$ (x $10^3$ $t$) | 0.00 | 3.84 | 4.38 | 4.67 | 4.76 |
| $-lnL$ | -14.58 | -16.41 | -17.64 | -17.76 | -17.43 |
| $SLOPE$ (%) | -0.24 | 3.03 | 3.78 | 4.64 | 2.83 |

(b) $M = 0.28$ yr$^{-1}$

| Quantity | $h$ = 0.2* | $h$ = 0.4 | $h$ = 0.6 | $h$ = 0.8 | $h$ = 1.0 |
|---|---|---|---|---|---|
| $K^s$ (x$10^3$ $t$) | 220.7 | 118.4 | 96.9 | 83.4 | 80.8 |
| $SB_{95}$ (x$10^3$ $t$) | 65.5 | 62.1 | 66.3 | 62.8 | 65.8 |
| $SB_{95}/K^s$ | 0.30 | 0.52 | 0.68 | 0.75 | 0.82 |
| $SB_{95}$ / $SB_{77}$ | 0.80 | 1.97 | 3.11 | 3.92 | 4.12 |
| $SB_{95}$ / $SB_{MSY}$ | 0.40 | 1.75 | 2.54 | 3.05 | 3.25 |
| $F_{MSY}$ | 0.00 | 0.21 | 0.48 | 0.83 | 1.16 |
| $C_{MSY}$ (x$10^3$ $t$) | 0.00 | 4.01 | 5.13 | 5.45 | 5.81 |
| $MSYR$ (%) | 0.00 | 11.31 | 19.67 | 25.94 | 29.64 |
| $F_{0.1}$ | 0.00 | 0.15 | 0.25 | 0.31 | 0.36 |
| $C_{0.1}$ (x$10^3$ $t$) | 0.00 | 3.89 | 4.74 | 4.97 | 4.98 |
| $0.1R$ (%) | 0.00 | 8.67 | 12.87 | 14.97 | 16.52 |
| $F_{SB50}$ | 0.00 | 0.09 | 0.14 | 0.18 | 0.20 |
| $C_{SB50}$ (x$10^3$ $t$) | 0.00 | 3.25 | 3.82 | 4.06 | 4.02 |
| $-lnL$ | -16.08 | -18.11 | -18.33 | -18.04 | -17.71 |
| $SLOPE$ (%) | -0.16 | 3.42 | 3.53 | 2.69 | 1.77 |

* $h$ = 0.2001 was used in the analysis, as the stock-recruitment relationship is undefined when $h$ = 0.2.

Table 6.5

Estimates, bootstrap CVs and percentile method 95% confidence intervals (CI) for 12 management-related quantities for the "base case" analysis for two choices of the instantaneous rate of natural mortality, $M$. Results are shown for analyses which consider uncertainty in steepness and which assume that steepness is known and equal to its maximum likelihood estimate.

(a) $M$=0.2 yr$^{-1}$ ($-lnL$ = -18.01)

| Quantity | Point | Steepness estimated | | Steepness fixed | |
|---|---|---|---|---|---|
| | Estimate | CV | 95% CI | CV | 95% CI |
| $K^s$ (x$10^3$ $t$) | 113.6 | 37.9 | [ 94.4, 274.9] | 15.5 | [ 109.9, 169.7] |
| $SB_{95}$(x$10^3$ $t$) | 76.6 | 39.9 | [ 24.6, 149.0] | 27.7 | [ 69.0, 142.8 ] |
| $SB_{95}/K^s$ | 0.66 | 33.9 | [ 0.17, 0.85 ] | 10.7 | [ 0.63, 0.84 ] |
| $SB_{95} / SB_{77}$ | 2.96 | 74.6 | [ 0.82, 6.38 ] | 21.4 | [ 1.61, 3.28 ] |
| $SB_{95} / SB_{MSY}$ | 2.32 | 50.9 | [ 0.36, 3.31 ] | 10.7 | [ 2.19, 2.94 ] |
| $H$ | 0.65 | 45.4 | [ 0.20, 0.90 ] | - | - |
| $C_{MSY}$ (x$10^3$ $t$) | 5.61 | 56.0 | [ 0.00, 7.93 ] | 15.5 | [ 5.36, 8.28 ] |
| $C_{0.1}$ (x$10^3$ $t$) | 5.20 | 54.8 | [ 0.00, 6.30 ] | 15.5 | [ 5.00, 7.72 ] |
| $C_{SB50}$ (x$10^3$ $t$) | 4.47 | 53.8 | [ 0.00, 5.84 ] | 15.5 | [ 4.31, 6.65 ] |
| $MSYR$ (%) | 17.01 | 68.9 | [ 0.00, 24.0 ] | - | - |
| $0.1R$ (%) | 10.95 | 62.1 | [ 0.00, 13.8 ] | - | - |
| $SLOPE$ (%) | 3.86 | 78.6 | [-0.78, 7.88 ] | 24.8 | [ 2.06, 5.06 ] |

(b) $M$=0.28 yr$^{-1}$ ($-lnL$ = -18.46)

| Quantity | Point | Steepness estimated | | Steepness fixed | |
|---|---|---|---|---|---|
| | estimate | CV | 95% CI | CV | 95% CI |
| $K^s$ (x$10^3$ $t$) | 96.9 | 39.2 | [75.4, 236.9] | 16.8 | [ 86.1, 134.6 ] |
| $SB_{95}$(x$10^3$ $t$) | 65.0 | 37.3 | [29.2, 129.6] | 30.0 | [ 54.0, 116.6 ] |
| $SB_{95}/K^s$ | 0.67 | 33.3 | [ 0.27, 0.82 ] | 12.9 | [ 0.63, 0.87 ] |
| $SB_{95} / SB_{77}$ | 3.10 | 61.6 | [ 0.82, 5.36 ] | 31.4 | [ 1.66, 4.08 ] |
| $SB_{95} / SB_{MSY}$ | 2.47 | 49.6 | [ 0.39, 3.06 ] | 12.9 | [ 2.18, 3.01 ] |
| $H$ | 0.59 | 40.9 | [ 0.20, 0.85 ] | - | - |
| $C_{MSY}$ (x$10^3$ $t$) | 5.05 | 55.9 | [ 0.00, 5.60 ] | 16.8 | [ 4.75, 7.43 ] |
| $C_{0.1}$ (x$10^3$ $t$) | 4.64 | 55.1 | [ 0.00, 5.37 ] | 16.8 | [ 4.37, 6.83 ] |
| $C_{SB50}$ (x$10^3$ $t$) | 3.81 | 63.3 | [ 0.00, 4.80 ] | 16.8 | [ 3.58, 5.60 ] |
| $MSYR$ (%) | 19.19 | 68.5 | [ 0.00, 27.1 ] | - | - |
| $0.1R$ (%) | 12.49 | 54.5 | [ 0.00, 14.0 ] | - | - |
| $SLOPE$ (%) | 3.65 | 75.7 | [-1.06, 6.18 ] | 36.2 | [ 1.48, 5.38 ] |

Table 6.6
Estimates of seven management-related quantities obtained from the "base case" analyses and the seven sensitivity tests. Results are shown for two choices for the instantaneous rate of natural mortality, *M*.

| *M* ($yr^{-1}$) | $K^s$ (x$10^3$ *t*) | $SB_{95}$ (x$10^3$ *t*) | $SB_{95}/K^s$ | $C_{MSY}$ (t) | *MSYR* (%) | $SB_{95}/SB_{MSY}$ | $SB_{95}/SB_{77}$ |
|---|---|---|---|---|---|---|---|
| "Base case" analysis | | | | | | | |
| 0.2 | 119.5 | 71.1 | 0.60 | 5.07 | 14.65 | 1.93 | 2.57 |
| 0.28 | 91.5 | 63.3 | 0.69 | 5.19 | 13.60 | 2.62 | 3.70 |
| Use inverse variance weighted average biomass series | | | | | | | |
| 0.2 | 101.6 | 58.5 | 0.57 | 5.28 | 18.39 | 2.04 | 4.69 |
| 0.28 | 88.8 | 52.6 | 0.59 | 4.59 | 17.65 | 2.02 | 3.61 |
| Trawl selectivity for biomass indices | | | | | | | |
| 0.2 | 143.4 | 109.8 | 0.77 | 6.50 | 15.07 | 2.54 | 1.90 |
| 0.28 | 145.4 | 121.6 | 0.84 | 6.81 | 15.61 | 2.79 | 1.59 |
| $a_m$ = 3 years | | | | | | | |
| 0.2 | 126.5 | 79.6 | 0.63 | 5.60 | 13.63 | 1.94 | 2.37 |
| 0.28 | 100.8 | 72.9 | 0.73 | 5.82 | 17.95 | 2.25 | 2.67 |
| $a_m$ = 5 years | | | | | | | |
| 0.2 | 105.5 | 70.4 | 0.67 | 4.75 | 16.72 | 2.48 | 3.37 |
| 0.28 | 83.4 | 55.5 | 0.67 | 3.73 | 16.91 | 2.52 | 3.58 |
| $a_{50}^T$ = 4 years | | | | | | | |
| 0.2 | 113.6 | 71.7 | 0.63 | 4.43 | 12.92 | 2.09 | 3.19 |
| 0.28 | 88.8 | 65.2 | 0.73 | 3.94 | 14.63 | 2.42 | 3.61 |
| $a_{50}^T$ = 2.7 years | | | | | | | |
| 0.2 | 125.5 | 71.8 | 0.57 | 3.48 | 8.84 | 1.84 | 2.52 |
| 0.28 | 88.8 | 63.7 | 0.72 | 2.25 | 5.00 | 2.42 | 3.82 |
| Knife-edged selectivity | | | | | | | |
| 0.2 | 113.6 | 74.6 | 0.66 | 5.56 | 18.09 | 2.48 | 3.02 |
| 0.28 | 94.2 | 63.5 | 0.67 | 5.04 | 20.08 | 2.53 | 2.98 |

Table 6.7
Annual catches (*t*) (1984 - 1995) of *Pterogymnus laniarius* by three South African fisheries.

| Year | Offshore linefishery | Inshore trawlfishery | Deep-sea trawlfishery | Total |
|---|---|---|---|---|
| 1984 | 78.0 | 625.4 | 60.7 | 764.1 |
| 1985 | 83.6 | 565.8 | 68.9 | 718.2 |
| 1986 | 83.5 | 519.4 | 311.5 | 914.4 |
| 1987 | 171.9 | 629.9 | 210.3 | 101.2 |
| 1988 | 213.9 | 553.0 | 220.7 | 987.6 |
| 1989 | 228.5 | 545.6 | 153.9 | 928.1 |
| 1990 | 171.6 | 328.0 | 143.6 | 643.2 |
| 1991 | 186.8 | 395.2 | 65.5 | 647.4 |
| 1992 | 273.0 | 448.1 | 106.3 | 827.4 |
| 1993 | 263.1 | 740.9 | 122.7 | 1126.6 |
| 1994 | 155.9 | 445.1 | 87.1 | 688.1 |
| 1995 | 200.0 | 531.7 | 76.5 | 808.2 |
| Mean catch | 75.8 | 527.3 | 135.6 | 838.8 |
| *SLOPE* | 7.2% | -1.4% | -5.1% | -0.2% |

The confidence intervals for the case in which steepness is assumed to be known without error are notably narrower that those for the case in which steepness is treated as a free parameter. This highlights the need for research into the productivity of species which have similar life history characteristics as panga. This could place plausible bounds on steepness to reduce uncertainty. Bayesian estimation techniques (e.g. McAllister et al., 1994; Walters and Ludwig, 1994) could also be used to incorporate auxiliary information such as estimates of steepness for other sparids into the assessment formally.

*Production modelling - sensitivity examination*

The results of the sensitivity tests are summarised together with those for the "base case" analysis in Table 6.6. Qualitatively, the results of the sensitivity tests are the same as those of the "base case", in that the current spawner biomass is estimated to be larger than what it was in 1977 and that at which *MSY* is achieved. *MSY* was estimated to be greater than current levels of catch. There are, however, some important quantitative impacts of changing the values of some of the model parameters.

The results are notably more optimistic in terms of the biomass of the stock, the status of the stock relative to $SB_{\mathrm{MSY}}$ and *MSY* if the selectivity for the biomass surveys is assumed to be the same as that for the inshore trawl fleet. However, the extent of recovery, as measured by the ratio $SB_{95}/SB_{77}$, is less optimistic. Decreasing the age-at-50%-selectivity from 5.5 years to 4 and then to 2.7 years leads to marked reductions in *MSY* and the fishing mortality at which the population is predicted to collapse (Table 6.6, Fig. 6.4). The latter occurs because the current selectivity pattern provides a "refuge" for spawners between the age-at-maturity and the age-of-50%-selectivity to the trawlfishery. The estimate of *MSY* increases if $a_{\mathrm{m}}$ is assumed to be 3 years and decreases if $a_{\mathrm{m}}$ is assumed to be 5 years. The former occurs because by decreasing the age-at-maturity from 4 to 3 years, the "refuge" between the age-at-maturity and the age-at-50%-selectivity is increased.

## Discussion

The results suggest that the panga stock has recovered substantially since the late 1970's when it was considered to be overexploited (Sato, 1980). The recovery from 20% of pristine levels of biomass to roughly 60 - 70% of this level is a consequence of reduced catches over the past two decades. The point estimates of current biomass are greater than estimated target levels for fisheries management. In this regard, there seems to be little need for advocating management strategies designed to guarantee a high probability of further recovery. Indeed, there may be an opportunity for increased catches of panga.

Table 6.8
Performance measures for a variety of possible future time sequences of catches from 1996. Results are shown for projection periods of 5, 10 and 20 years for the case in which $M = 0.28$ yr$^{-1}$ and the steepness parameter is estimated.

| Future catch (*t*) | $P(SB_y < SB_{95})$ | $P(SB_y > SB_{\mathrm{MSY}})$ | $P(SB_y > SB_{0.1})$ |
|---|---|---|---|
| $C = 839$ | | | |
| $y = 5$ | 0.19 | 0.82 | 0.80 |
| $y = 10$ | 0.19 | 0.82 | 0.79 |
| $y = 20$ | 0.20 | 0.81 | 0.79 |
| $C = 4000$ | | | |
| $y = 5$ | 0.39 | 0.75 | 0.70 |
| $y = 10$ | 0.47 | 0.74 | 0.67 |
| $y = 20$ | 0.50 | 0.73 | 0.65 |
| $C = 5000$ | | | |
| $y = 5$ | 0.59 | 0.73 | 0.64 |
| $y = 10$ | 0.80 | 0.65 | 0.62 |
| $y = 20$ | 0.85 | 0.62 | 0.60 |
| $C = 6000$ | | | |
| $y = 5$ | 0.84 | 0.69 | 0.55 |
| $y = 10$ | 1.00 | 0.61 | 0.55 |
| $y = 20$ | 1.00 | 0.61 | 0.53 |
| $C = 7000$ | | | |
| $y = 5$ | 1.00 | 0.62 | 0.55 |
| $y = 10$ | 1.00 | 0.58 | 0.50 |
| $y = 20$ | 1.00 | 0.55 | 0.40 |

Table 6.9
Estimates of biological reference points. Catch units are metric tons. "NE" indicates that the quantity was not estimated by the study concerned.

| Stock assessment technique | Biological reference point | | | | | | |
|---|---|---|---|---|---|---|---|
| | $M$ | $F_{MSY}$ | $C_{MSY}$ | $F_{0.1}$ | $C_{0.1}$ | $F_{SB50}$ | $C_{SB50}$ |
| Surplus production model[1] | - | NE | 6800 | NE | NE | NE | NE |
| Yield-per-recruit[1] | 0.2 | 0.28 | 5200 | 0.19 | 5000 | NE | NE |
| Yield-per-recruit[2] | 0.2 | NE | NE | 0.25 | 6443 | 0.20 | 5707 |
| | 0.28 | NE | NE | 0.39 | 4302 | 0.30 | 3924 |
| Age-structured production model[3] | 0.2 | 0.31 | 5610 | 0.17 | 5200 | 0.11 | 4470 |
| | 0.28 | 0.47 | 5050 | 0.24 | 4640 | 0.14 | 3810 |

[1]Sato (1980); [2]Chapter 5; [3]Present study

One biological attribute of the panga that mitigates against rapid stock rebuilding is its slow growth. This attribute is characteristic of fishes of the family Sparidae (Chapter 3) and contributes to a relatively low production to biomass ratio and yield-per-recruit. Other, and possibly more, important biological characteristics of panga contribute to its resilience to exploitation and its ability to recover from overexploitation. These include a late gonochoristic reproductive style (functionally gonochoristic with all immature fish passing through an intersexual stage before sexual differentiation and maturation) and protracted year round spawning throughout its distributional range. The panga also feeds predominantly on soft sediment associated prey, such as the brachyurans *Gonoplax angulata* and *Mursia cristimanus* (Chapter 3). As the Agulhas Bank consists of large areas of unconsolidated surficial sedimentary deposits interspersed with low relief reef with soft sedimentary depressions (Le Clus et al., 1994; 1996), the panga can exploit large areas throughout the Agulhas Bank (Chapter 4). Lastly, the panga is selected in all existing fisheries at an age at least 1.5 years after maturity.

*MSYR* measures the overall productivity of the population. The estimates of *MSYR* in Tables 6.4, 6.5 and 6.6 are higher than those for kingklip *Genypterus capensis* (Punt and Japp, 1994), and similar to those for the Cape hakes *Merluccius* spp. (Punt, 1994), two other demersal trawl species in South African waters for which comparable estimates are available. It may appear somewhat surprising that *MSYR* for panga is similar to that for the faster-growing shorter-lived hake and higher than for the faster-growing kingklip. However, this is probably a consequence of the selectivity pattern in the panga fishery. If the age-at-50%-selectivity was lower than at present, *MSYR* for panga would be lower than that for hake and kingklip.

It might have been anticipated that one sign of the recovery of the panga resource would have been an increase in catches. However, contrary to this expectation, panga catches have declined over recent years (Fig. 6.1; Table 6.7). There are several good explanations why panga catches have not increased. Panga is caught as a last resort in the offshore linefishery due to its small size, low market price and its preference for deeper water which makes fishing difficult. Despite this, there are moves towards catching more panga, particularly between Stil Bay and East London where presently it is numerically the second most important species landed (Brouwer, 1997). This increasing trend is primarily a consequence of a decline in the abundance of other larger target species (predominantly sparids and sciaenids) which have dominated this fishery in the past (Smale and Buxton, 1985; Hecht and Tilney, 1989). The steady decline in the catch of panga by the deepsea trawlfishery reflects not a change in the abundance of panga but rather a shift in directed fishing effort towards hake.

Trends in catch and catch rates for the deep-sea trawl fleet and the offshore linefishery are, therefore, clearly misleading as indices of panga abundance. By contrast, catch and catch rates for the inshore trawl fleet are probably more representative of panga abundance as there have been fewer changes to this fleet over the past decade and because catches of panga are incidental whilst targeting hake (and sole by some vessels operating from Mossel Bay). The inshore trawlfishery lands the largest proportion of the panga catch (>60%) although catches have shown a slight decrease over the past decade (Table 6.7). In this type of fishery, stock rebuilding would be evident if there was either an increase in catch with stable effort or a stabilisation of catch with a decrease in effort. As effort by the inshore trawl fleet has declined, the overall trend in catch rate is positive, although the rate of increase is less than for the biomass indices (Table 6.2).

Panga favour areas that are not fully accessible to conventional otter trawling gear. The best trawl catches are made in winter after periods of rough weather, most notably after south- and north-westerly gales, which possibly displace panga from the hard grounds to areas more favourable to trawling (Capt. T. Morris, pers. commn.). In the past (pre-1970's), trawlers used to direct effort towards panga after periods of rough weather in anticipation of profitable catches. Since the decrease in panga abundance between 1970 and 1980, trawl effort is now concentrated on hake- and horse mackerel-dominated areas. The observed low rate of increase in the catch rate of panga for the inshore trawlfishery could possibly be explained by this shift in effort.

The impact of future catches can be assessed by projecting the estimated age-structure at the start of 1996 under a variety of possible future catch scenarios (Fig. 6.5; Table 6.8). The data in Fig. 6.5 show deterministic projections from the "base case" point estimates while the results in Table 6.8 are based on the results of bootstraps which consider uncertainty about steepness. The statistics used to quantify performance are the probability that the spawner biomass drops below the current level, the probability that the spawner biomass is above that at which $C_{MSY}$ is achieved, and the probability that the spawner biomass is above that at which $C_{0.1}$ is achieved. Future catch levels equal to the average South African catch over the last ten years (839 *t*) as well catches as of 4000, 5000, 6000 and 7000 *t* are considered. 5000 *t* is approximately the estimate of *MSY* from this study, while the upper limit of 7000 *t* corresponds approximately to the estimate of *MSY* obtained by Sato (1980) from a surplus production model (Table 6.9). The range of catches considered, therefore, encompasses the range of yields predicted from previous assessments. The analysis of potential yield and the impact of future catches is based on a trawl-based panga-directed fishery. Consideration might be given in the future to a hook-based panga fishery if increases in catches of panga are independent of increased catches of sympatric species such as hake *Merluccius capensis*. Although not shown here, the implications for a hook-based fishery of catches in the range of 800 to 7000 *t* are qualitatively the same as those for a trawl-based fishery.

Qualitatively, the results of the risk analysis suggest that under a regime of catches equal to the average South Africa catch over the last decade, the resource should continue to increase (Fig. 6.5). Catches exceeding 4000 *t* should lead to a better than even chance of the biomass dropping below its current level within five years. The probability of dropping below $SB_{\mathrm{MSY}}$ and $SB_{0.1}$ increases with an increasing level of catch, although even over a 20-year projection period, these probabilities do not exceed 0.5 except for the 7000 *t* catch scenario. This is probably because $SB_{\mathrm{MSY}}$ and $SB_{0.1}$ are estimated to be small fractions of $K^s$ (Fig. 6.5) and the current biomass is estimated to be well above this level (Table 6.5). Naturally, catches larger than *MSY* are unsustainable over the long term.

The results in Table 6.8 and Figure 6.5 could be used by decision makers to select appropriate management measures for this resource. However, we believe that the most appropriate approach to its future management is the use of a management procedure. A management procedure is the combination of an assessment method (such as the age-structured production model) and a harvest strategy (a method for specifying a management measure using the results of the assessment). To date, management procedures have been developed for the anchovy *Engraulis capensis* (Butterworth and Bergh, 1993; Butterworth et al., 1993) and Cape hake *Merluccius* spp. (Punt, 1993a) resources in South Africa.

The precautionary principle must prevail, with caution to be taken before substantial increases in catch are permitted. For example, the data are uninformative about the value of the steepness parameter to which the results are highly sensitive (Tables 6.4 and 6.5). The estimates of long-term sustainable yield are also very sensitive to assumptions about the age-at-50%-selectivity for the trawl fleet (Table 6.6; Figure 6.4). Furthermore, catch rate data for the hake directed inshore trawlfishery (Table 6.2) suggest a much slower rate of increase than the fishery-independent trawl surveys. Whilst the surveys are more likely to provide a more representative index of abundance, the possibility that the fishery independent index is biased cannot be ignored. One of the assumptions underlying the analyses in this study is that the unexploited equilibrium level is the same as it was in 1898. Walters (1986) provides a variety of scenarios which may lead to nonstationarity of the underlying production relationship. In particular, habitat modification may have reduced the unexploited equilibrium level of panga because favoured areas of panga habitat include hard grounds (low and high profile reef) interspersed with unconsolidated sediments. These habitats have well established benthic communities, consisting predominantly of hard corals, sponges and bryozoans (Badenhorst and Smale, 1991). It is suspected that these could have been severely damaged by the bobbin and rockhopper trawl gear which were used extensively by the large foreign trawlers. This gear effectively crushes all obstacles in the path of the net. If such changes in habitat and hence unexploited equilibrium level have occurred, the projections which suggest further increases in population size may be over-optimistic.

Table 6.10
The status of various commercially important South African sparid species. SFRI = Unpublished data from the Sea Fisheries Research Institute, Cape Town.

| Species | Common name | Status | Source |
|---|---|---|---|
| *Cheimerius nufar* | Santer | Fully exploited | SFRI |
| *Chrysoblephus cristiceps* | Dageraad | Overexploited | Buxton (1992) |
| *Chrysoblephus laticeps* | Red Roman | Overexploited | Buxton (1992) |
| *Chrysoblephus puniceus* | Slinger | Overexploited | Punt et al. (1993) |
| *Cymatoceps nasutus* | Poenskop | Overexploited | SFRI |
| *Lithognathus lithognathus* | White steenbras | Overexploited | Bennett (1993) |
| *Pachymetopon blochii* | Hottentot | Fully exploited | Pulfrich and Griffiths (1988b); Punt et al. (1996) |
| *Petrus rupestris* | Red steenbras | Overexploited | Garratt (1985); Smale and Punt (1991); SFRI |
| *Polysteganus praeorbitalis* | Scotsman | Overexploited | Garratt(1985); SFRI |
| *Polysteganus undulosus* | Seventy-four | Overexploited | Garratt (1985); SFRI |
| *Pterogymnus laniarius* | Panga | Recovering | This study |

The estimates of yield from Chapter 5 and this study are generally lower than those of Sato (1980), because the growth parameters used in his analysis were based on scales and were found to be inaccurate (overestimating growth rate). In addition, fish were recruited 3 years before maturation into the foreign trawlfishery (because of liners within the cod-end of the net). The estimates of $F_{0.1}$ and $F_{SB50}$ (the fishing mortality at which the spawning biomass is reduced to half its pristine level) in this study are notably lower than those in Chapter 5 because this approach takes account of a stock-recruitment relationship whereas the estimates using yield-per-recruit modelling (see Chapter 5) were based implicitly on the assumption that $h = 1$.

The yield estimates in Chapter 5 were based on multiplying an estimate of yield-per-recruit by an estimate of 0-year recruitment, derived from Sato's (1980) cohort analysis. Although the estimates of fishing mortality were lower (when $M = 0.28$ yr$^{-1}$) in this study, the estimates of recruitment were higher than Sato's (1980). This results in a yield estimate higher than those using yield-per-recruit (Chapter 5). The $F_{SB50}$ and $F_{0.1}$ reference points considered in Chapter 5 attempt to deal with both spawner biomass-per-recruit and yield- per-recruit. Steepness is, however, assumed to be equal to 1 in the per-recruit analysis resulting in the increased productivity and resilience of the stock.

Paucity of data prevents any comprehensive conclusions to be drawn about the status of sparid fisheries world-wide. However, considerable information is available for the commercially important sparid species in South Africa (Table 6.10). It appears that the status of many sparid stocks are poor, with most species currently overexploited. South Africa has a diverse sparid fauna comprising 41 species, of which 25 are endemic. These species make an important contribution to the trawl and linefisheries. Despite their importance within the commercial and recreational sectors, sparid life-history characteristics such as longevity, slow growth, residency, sex-change and barotrauma contribute to making sparid species unsuitable candidates for high levels of exploitation (see Chapter 3). With respect to habitat preferences, South African sparids are generally restricted to areas of high relief reef. This includes species such as the red roman *Chrysoblephus laticeps*, dageraad *Chrysoblephus cristiceps*, slinger *Chrysoblephus puniceus*, red stumpnose *Chrysoblephus gibbiceps* and poenskop *Cymatoceps nasutus* (Smith and Heemstra, 1986). This is in contrast to the panga's ability to exploit vast areas of soft ground and low-profile reef. A combination of greater available area of habitat to colonise, suitable life history characteristics, the absence of a directed fishing and the cessation of foreign trawling effort would suggest that some form of rebuilding has taken place within the stock. When seen in this context, the panga appears to be a sparid species showing signs of recovery and the ability to sustain a higher fishing pressure in the future.

# Chapter 7 – General discussion with considerations on the management of bycatch resources on the Agulhas Bank and on the development of a directed fishery for panga

## Introduction

From the procedure outlined in Chapter 1, management information obtained using different methods have varying levels of resolution. Depending on the required objectives, by careful planning of the different methods, the level of resolution needed for the management of the resource in question can be customised. For example, after concluding a biological study on a species, the information obtained may or may not be sufficient to ensure rational and sustainable management. Similarly, whilst suitable biological reference points can be estimated for a bycatch species they might not be sufficient to ensure effective management, as levels of catch rather than fishing effort are required to manage the resource. Obviously, the more time and effort (and money) that is invested into studying a resource, either from a biological and/or modelling perspective, the better the chances are for sustainable management. Research on bycatch is more often than not limited by short-term funding and the need to provide management advice is derived from limited data. It is, therefore, necessary to carefully define the most suitable approach to effectively derive the optimum management related information.

An updated and refined flowchart of the procedure outlined in Chapter 1 is presented in Figure 7.1. The procedure described is general in that it can used to facilitate the management of other bycatch species. It summarises the research process, what initial basic information is required and what outputs can be obtained at each stage. As one progresses through the flowchart the research becomes more dependent on previous studies. It is for this reason that if the resource is to be modelled at a later date, pertinent auxiliary information such as abundance indices, *CPUE* estimates and other catch statistics must be collected from the initiation of the study.

The question arises as to what pertinent information is available at each level in the proposed procedure. When the decision to manage the resource is made, a bycatch assessment and management program needs to be initiated. A two-pronged approach should then be undertaken depending on the defined management objectives (Fig. 7.1). Firstly, a full biological study needs to be undertaken to obtain an insight into the life history of the species (Chapter 3). This should provide information on longevity and growth rate and complete information concerning its reproductive biology. Investigations into its feeding biology will reveal any possible competition for food resources, and whether or not it consumes similar prey to other sympatric species. An understanding of the spatial aspects of the resources' distribution and abundance can provide information on the possible existence and locality of nursery areas and any ontogenetic related migratory patterns (Chapter 4). Simultaneously, a concerted effort is needed to collect primary fishery statistics on the resource such as *CPUE* and species composition of the catch. Auxiliary information such as abundance indices should also be collected. These data can be used later in modelling the fishery. If modelling the resource is necessary then two approaches can be followed, each with it's own inherent advantages and disadvantages. The choice is to either adopt a per-recruit (Chapter 5) and/or age-structured modelling (Chapter 6) approach. These are merely determined by the availability of suitable information as input parameters. If basic biological and fishery parameters are available then the former approach is feasible, however, the latter is only possible if auxiliary fisheries data are also available. It must be noted that there is considerable feedback and interaction between the modelling of the resource and the continual collection of biological/auxiliary information. This is necessary to tune the more complicated and integrated fisheries models in addition to providing meaningful quantitative results (Chapter 6). Finally, using the most suitable stock assessment model, an Operational Management Procedure can be developed.

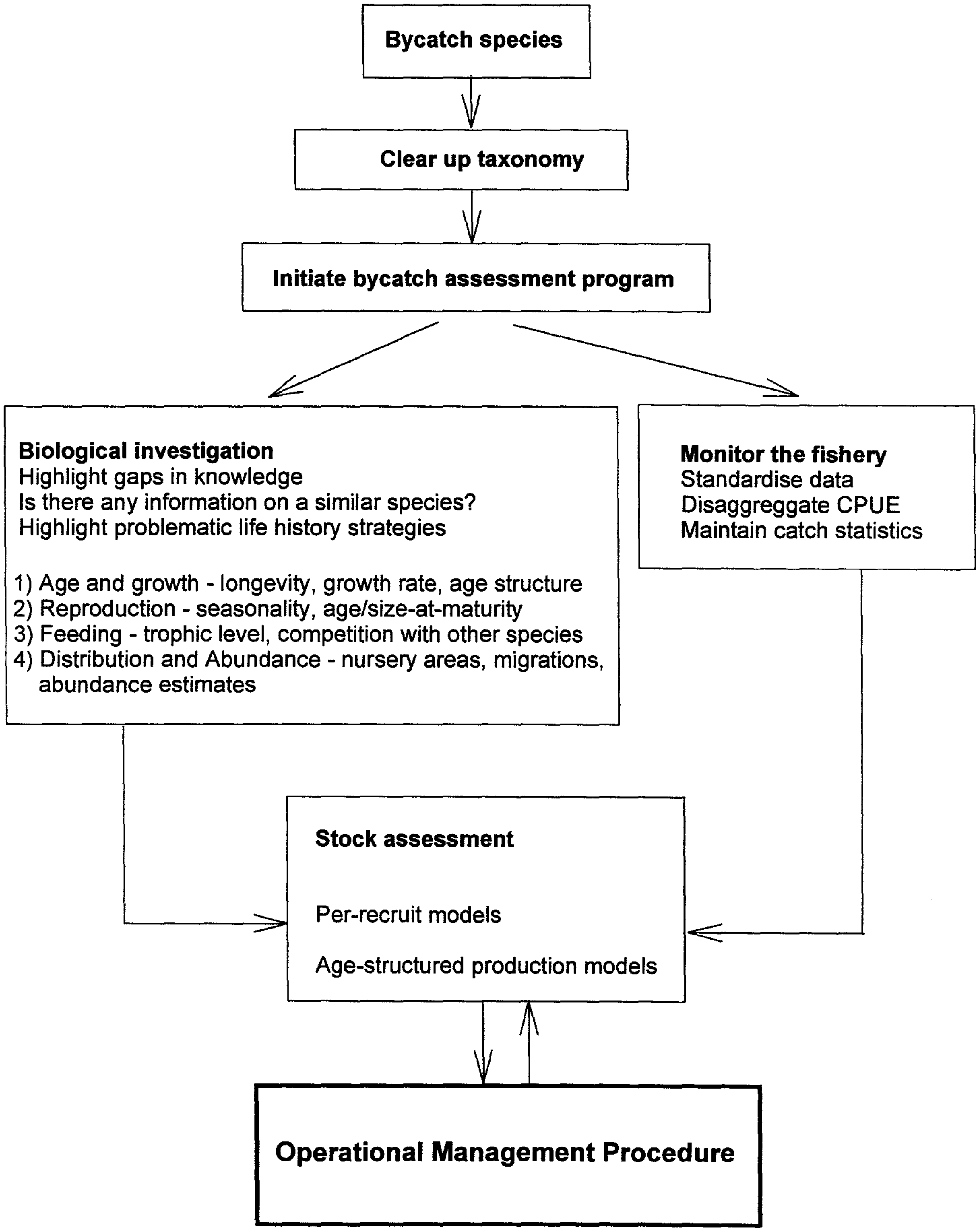

Fig. 7.1 Updated flowchart of a proposed bycatch management strategy

The most comprehensive research previously undertaken in South Africa on a bycatch species is on the kingklip *Genypterus capensis*. This is mainly due to its high market value, which led to a directed longline fishery that briefly operated between 1982 and 1990. Aspects regarding the directed fishery (Japp, 1989; Japp and Punt, 1989), the kingklip's biology (Japp, 1989) and status (Japp and Punt, 1989; Punt and Japp, 1994) are well documented. Limited information is, however, available on its distribution and abundance. This is principally due to its preference for hard grounds, in particular deep and high-profile reef. It is for this reason that auxiliary *CPUE* data, used to tune the age structured model described by Punt and Japp (1994), were found to be preferable as an abundance index to the biannual biomass survey estimates. The panga is similar in many respects to the kingklip. Both have been targets of a directed fishery in the past and both prefer hard grounds that are relatively inaccessible to conventional trawling gear. In the case of panga, relative biomass estimates were the only suitable abundance estimate available for integrated modelling.

This thesis has attempted to make a contribution towards the development of a suitable method, which can investigate both spatial patterns in fish distribution and abundance and facilitate the estimation of detrended relative biomass estimates. This was achieved by developing a Geographical Information System which is new, both in South Africa and internationally. This thesis, therefore, makes a significant contribution in this field and provides a statistically robust platform to enable the integration of existing stock assessment methods within a spatial analysis framework. The GIS developed in this study is the first step in the development of a Fisheries Information Systems (FIS) for the Agulhas Bank which could, in the next 5 years, be used in both the analysis of resource distribution patterns and in their management. The FIS will be able to analyse and integrate disparate types of fishery related information so that resources and their various fisheries can be simultaneously managed. In the recent White Paper on a new policy for South African fisheries (Anon., 1997), Vessel Monitoring Systems will be installed on fishing vessels in the near future. These will link the geographical position of the vessel and its operational status (i.e. fishing, steaming or anchoring) via satellite to a designated ground station. Such a FIS will, therefore, provide a suitable real-time, spatial management system and facilitate integrated resource management. Another GIS, currently being planned, which can be incorporated into the FIS is to investigate habitat types on the Agulhas Bank and to quantify associated fish assemblages. This is necessary as the sedimentological data available is patchy and the distribution of areas of low and high profile reef are largely unknown. Analysing these data from a spatial perspective can provide considerable insight into multispecies fisheries, contributing to understanding the root cause of most bycatch problems. For example, if a haul contains various species their presence in the net could be due to one of two factors. Either the species are sympatric with the haul reflecting the composition of the fish assemblage or the fish are allopatrically distributed and associated with a particular habitat. In the latter scenario, as the gear passes through a variety of habitat types it would catch an apparently multispecies fish assemblage. The solution to the latter scenario would be to minimise trawling across habitat types thereby reducing bycatch within the fishery.

### Managing the panga resource

The stock assessment models used in this study have suggested that a substantial increase in yield of panga would be sustainable on the Agulhas Bank. Even under present catch levels, there appears to be evidence for a stock recovery (Chapter 6). This implies that if panga were to remain a bycatch in the trawlfisheries, no new management strategy would be necessary. Alternatively, the panga stock can be fished in some new directed fishery. In the latter scenario considerations must be given to existing catches by the trawlfisheries.

Questions obviously arise as to whether or not it is actually possible to develop a panga directed fishery to exploit the resource at maximum sustainable levels. If such a fishery were developed, what gear should be used and what areas should be fished? The impact of a panga directed fishery on sympatric species, particularly those that are part of current directed fisheries and which are subject to quota restrictions also needs to be assessed. In the scenario where panga is caught within both the directed fishery and as bycatch in the trawlfisheries, similar questions arise regarding possible bycatch problems, gear selection and potentially fishable areas.

Problems are inherent in the development of a new directed fishery, particularly on a resource that has been landed as bycatch in the past. Intuitively, if a species makes up a significant proportion of the bycatch within a multispecies fishery and is developed into a directed fishery, it will have its own inherent bycatch problems. Therefore, suitable data is needed to address this issue. As there is presently little information regarding bycatch and discarding rates, other available data on the resource should be used.

If a panga directed fishery were to be developed, estimates of bycatch would need to be ascertained in order to minimise any potential impact that the fishery might have on other sympatric species. A first estimate of the approximate contribution of the various species caught within a panga directed fishery needs to be determined. The most suitable data source is that of the research surveys conducted by the joint Japanese/South African biomass surveys (Uozumi et al., 1981; 1985; Hatanaka et al., 1983) and those obtained from the biannual SFRI biomass surveys. Similarly, catch data from the linefishers who direct effort towards panga collected between 1994 and 1996 are available.

An inherent problem of the combined South African and joint Japanese/South African dataset is the fact that not all possible panga habitats were sampled. Whilst the current South African surveys did not cover most of the hard grounds of the Agulhas Bank, the previous joint Japanese/South African biomass surveys covered extensive areas, with the exception of the high-relief reef which cannot be trawled with bobbin trawl gear. A suitable method was developed in this thesis to obtain a first approximation of the fish assemblage associated with those areas that were dominated by panga. The relative contribution by mass of the various species within the ichthyofaunal assemblage was estimated to provide some quantitative indication of whether or not a bycatch problem would emerge in a panga directed fishery.

This method is new and fulfils the preliminary purpose of assessing possible bycatch problems before a more detailed GIS becomes available to address this issue.

The method used is described as follows. Those trawls that were dominated by panga (where panga constituted the greatest relative mass in each trawl) were selected and the percentage mass composition of all species noted. The geographic location of each trawl was also noted. This method was also applied to the commercial and recreational linefish catches where panga was the dominant species.

Of the 1585 research trawls analysed, 126 (8%) were found to be dominated by panga irrespective of the percentage mass of the other constituent species and in 56 trawls panga constituted at least 40% of the total trawl mass. The distribution of these trawls and the relative proportions of each of the major constituent fish species are described in Figure 7.2 and Table 7.1. Of the linefish catches dominated by panga, panga constituted on average 68% of the total catch. Six other sympatric species were present in the catches, each with a contribution of at least 0.5%.

From the trawl data, the depth distribution of the areas dominated by panga ranged between 50 and 150 m (Figure 7.2) in two principal areas. These areas were on the Central Agulhas Bank between 50 and 100m and off Mossel Bay at approximately 100m. Other areas that were also dominated by panga but to a lesser degree were off Port Elizabeth and Cape St Francis. The proportion of panga within both the commercial and recreational linefish catches was found to be significantly higher than in the research trawls. This is simply a consequence of higher gear selectivity and the discarding of undesirable species. In the research trawls in the two areas there were up to 20 sympatric species, of which eight constituted more than 1% by mass (Table 7.1). The most important of these species was hake which constituted >11% of trawl biomass. These data suggest that despite trawling in an area dominated by panga, the fish assemblage collectively comprises of a biomass equal to or exceeding that of panga. This poses a problem with respect to possible high bycatch rates in a panga directed trawlfishery. Although the research trawls use a pilchard mesh (stretched mesh = 25 mm) liner in the cod-end, it can be assumed that fish would be caught in similar proportions with commercial gear as the selectivities of both gears are qualitatively similar (Japp et al., 1994).

Determining the limits of allowed bycatch within a directed fishery is both difficult to determine and is also fishery specific (Hall, 1996). To manage a directed fishery effectively, it is necessary that gear selectivity is high to reduce bycatch. It must be noted that in South Africa, no limits have been set on the level of acceptable bycatch within any directed fishery, therefore, prompting further research in this area.

### Overview of current and potential fishing methods for a panga directed fishery

In developing a new directed fishery it is necessary to consider the various fishing gears that are currently available and to assess their advantages and disadvantages in the light of management objectives. Management objectives would include the ability to fish the targeted species effectively and to limit the catch of other bycatch species. If current fishing gears are found to be unsuitable then consideration must be given to the development of alternative fishing gears. The panga stock has been harvested using a variety of gears each with its own inherent selectivities, efficiencies and limitations (Table 7.2). It is for this reason that the efficiency of these gear types and their ability to meet defined management objectives needs to be investigated. A study of this nature is obviously beyond the scope of this thesis. In the interim, a preliminary assessment can be made regarding their ability to catch panga and to possibly reduce levels of bycatch. Three gear types have been identified and are discussed as below.

#### *Nets*

Demersal trawling with otter trawls has been the principal method to catch this species in the past. East of Cape Agulhas, where panga is abundant, minimum stretched mesh regulations allow for the selection of fish larger than size-at-maturity (Chapters 5 and 6).

The foreign fleets that fished this resource in the past consisted of large deepsea vessels using otter trawling gear with bobbins/rock-hoppers. This gear type was found to unselective (Joint Japanese/South African Biomass Surveys 1980-1981, unpublished data) and during the period 1964 to 1977, despite panga being the targeted species, it only constituted approximately 14% of the total foreign trawl catch. Hake was the most important bycatch species at approximately 40% of the total trawl catch. This fact re-emphasises the unselective nature of otter trawling gear and its unsuitability as a method for directed effort. Otter trawling with bobbins is also suspected of damaging the substratum particularly on hard, low-profile panga dominated grounds with hard corals, bryozoans and sponges (Jones, 1992). Since the exclusion of these foreign vessels from South African waters in 1972 the panga stock has had an opportunity to rebuild (Chapter 6). It is, however, unlikely that the grounds have had a chance to recover, evidenced during the past decade by commercial SCUBA dive operators (H. van Niekerk, Port Elizabeth, pers. comm.). The use of bobbins and/or rock-hoppers in South African waters, which are currently legal up to 375mm in diameter, needs to be re-addressed until the impact that they have on the benthic community has been assessed.

*Hooks*

The use of small hook longlines or rod/handlines with which to target panga is an alternative and needs to be thoroughly investigated as a directed fishing method. Preliminary results of experimental small hook (2/0") longlining, revealed that panga only constituted 50% of the catch with hake being the dominant bycatch species (> 40%) (M. Craig, Robberg Fast Foods, Plettenberg Bay, pers. comm.). Despite placing the longlines on the substratum, a commonly used strategy to reduce the selectivity on hake, hake bycatch rates were not alleviated. This poses a serious problem as hake are restricted by quota. The use of small hooks could also increase the incidence of juvenile bycatch of many trawl and linefish species.

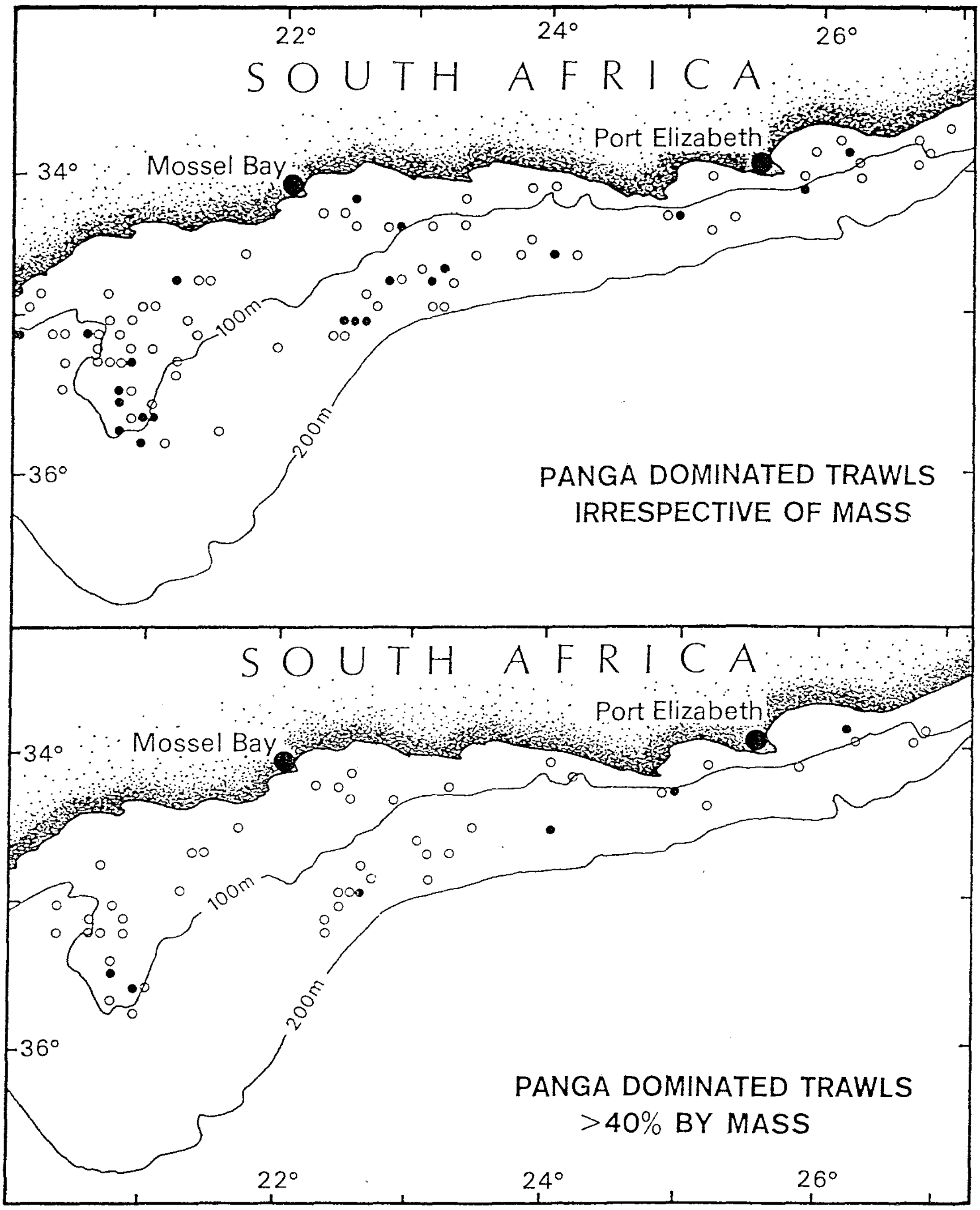

Fig 7.2 Map of the Agulhas Bank with trawl positions where *Pterogymnus laniarius* was either the dominant species irrespective of mass (n = 126) or where it represented at least 40% by total trawl mass (n = 59) of each trawl catch. Open and closed dots denote where one and greater than one trawl was dominated by *P. laniarius*. Data was extracted from 1585 research trawls conducted between Cape Agulhas and Port Alfred between 1980 and 1995.

Table 7.1
Percentage composition (± standard deviation) of fish species present in trawls either dominated by *Pterogymnus laniarius* irrespective of mass (n = 126) or where *P. laniarius* constituted >40% of the catch by mass (n = 56) and from commercial (n = 11) and recreational (n = 4) offshore linefish catches where *P. laniarius* was the dominant species by mass. Trawl estimates were obtained using biomass survey data (n=1585 trawls) from 1980-1995 and only species which contributed >5% by mass were chosen for the analysis. All species within the linefisheries were used for analysis. Only those species which were >0.5% of the various catches are shown below. CV = co-efficient of variation; 95% CI = 95% confidence interval.

| | | | Irrespective of mass | | | >40% by mass | | |
|---|---|---|---|---|---|---|---|---|
| Common name | Specific name | Fishery investigated | Mean±SD | CV(%) | 95% CI | Mean±SD | CV(%) | 95% CI |
| Panga | *Pterogymnus laniarius* | Research trawl | 40.0±12.6 | 31 | (37.8, 42.2) | 50.3±10.0 | 20 | (47.7, 52.9) |
| | | Commercial line | 68.6±14.3 | 450 | (40.6, 96.7) | | | |
| | | Recreational line | 73.8±13.9 | 841 | (19.0, 128.6) | | | |
| Hake | *Merluccius capensis* | Research trawl | 12.4±9.9 | 80 | (10.6, 14.1) | 11.2±9.2 | 82 | ( 8.8, 13.6) |
| | | Commercial line | 4.0±6.4 | 200 | (-8.4, 16.5 | | | |
| | | Recreational line | 8.3±16.7 | 830 | (-24.4, 41.1) | | | |
| Horse mackerel | *Trachurus t. capensis* | Research trawl | 6.4±8.4 | 131 | ( 5.0, 7.9) | 6.1±7.5 | 124 | ( 4.1, 8.0) |
| Spiny dogfish | *Squalus megalops* | Research trawl | 7.0±7.8 | 112 | ( 5.6, 8.4) | 4.4±6.7 | 153 | ( 2.7, 6.1) |
| Lesser gurnard | *Chelidonichthyes queketti* | Research trawl | 1.7±4.7 | 280 | ( 0.8, 2.5) | 0.2±1.0 | 539 | ( -0.1, 0.4) |
| Cape gurnard | *Chelidonichthyes capensis* | Commercial line | 3.4±4.2 | 140 | (-5.1, 11.9) | | | |
| | | Recreational line | 4.4±7.7 | 380 | (-10.6, 19.4) | | | |
| Carpenter | *Argyrozona argyrozona* | Research trawl | 1.3±3.9 | 298 | ( 0.6, 2.0) | 1.3±3.6 | 278 | ( 0.4, 2.2) |
| | | Commercial line | 11.8±11.5 | 360 | (-10.6, 34.3) | | | |
| | | Recreational line | 9.0±11.7 | 590 | (-14.0, 32.1) | | | |
| Silver Kob | *Argyrosomus inodorus* | Commercial line | 4.5±10.0 | 330 | (-15.7, 24.6) | | | |
| Santer | *Cheimerius nufar* | Commercial line | 1.8±2.3 | 73 | (-2.8, 6.3) | | | |
| Dageraad | *Chrysoblephus cristiceps* | Commercial line | 3.2±9.8 | 310 | (-15.6, 22.4) | | | |
| Windtoy | *Spicara auxillaris* | Research trawl | 0.9±4.7 | 499 | ( 0.1, 1.7) | 0.5±4.2 | 768 | ( -0.5, 1.6) |
| Sandcord | *Gonorhynchus gonorhynchus* | Research trawl | 0.7±3.4 | 522 | ( 0.1, 0.3) | 1.4±5.0 | 351 | ( 0.1, 2.7) |
| Jacopever | *Helicolenus dactylopterus* | Research trawl | 0.8±3.0 | 366 | ( 0.3, 1.3) | 0.7±2.6 | 395 | ( 0.0, 1.3 |
| Joseph shark | *Callorhynchus capensis* | Research trawl | 0.5±1.9 | 350 | ( 0.2, 0.9) | 0.3±1.3 | 444 | ( 0.0, 0.6) |

Table 7.2
Summary of the advantages and disadvantages of current and potential *Pterogymnus laniarius* fishing methods on the Agulhas Bank, South Africa.

| Method | Advantages | Disadvantages |
|---|---|---|
| Inshore otter trawl (standard) | Exploits fish > maturity with mesh 75mm, no need to change the fisheries gear or areas fished. | Cannot increase effort without risking high bycatch. Fish quality is poor as most fish are kept on ice for 7-10 days. |
| Deepsea otter trawl (with bobbins/rockhoppers) | Highly efficient for targeting panga over certain low profile reef and rocky substrata. | Bobbins are suspected of causing extensive damage to hard corals and other sensitive areas of panga habitat. There is a high bycatch problem of incidental species. Due to good freezing facilities the fish is generally of a good quality. |
| Hooks (offshore linefishery) | Exploits fish >> maturity; No need to change fishery; The fish is landed fresh and is of a good quality. Quality can be improve by proper handling. | It is difficult to fish at depths >50m and therefore fishers need high rewards for their effort. |
| Small hooked longlining | It may be possible to target the stock due to the relatively high gear selectivity; Excellent fish quality, particularly for the export market. | There is a high incidence of hake bycatch. |
| Fish traps | It is possible to target the stock effectively to maximise catch and minimise bycatch; Excellent fish quality for the export market. | There is the possibility of high bycatch. This is a new fishing technique which has not been used in South Africa before and will need refining to become effective. |

*Traps*

Another gear type that has not been tested or used for teleosts in South Africa is fish traps. These have been used successfully in many countries as they have both the ability to selectively target a particular species, whilst retaining a high quality product that can be marketed for export (Kailola et al., 1993). They have been found to be extremely effective for snapper *Pagrus auratus* in Australia (Kailola et al., 1993), a sparid of similar proportions to the panga. Concerning the bycatch problem, three principal quota restricted species need to be excluded; hake, kingklip and south coast rock lobster *Palinurus gilchristi*. It was found that panga constituted a substantial bycatch in the south coast rock lobster fishery in the past (C.J. Wilke, Sea Fisheries Research Institute, Cape Town, Pers. Comm.). The bycatch of other sympatric sparids such as the red stumpnose *Chrysoblephus gibbiceps*, santer *Cheimerius nufar* and blue hottentot *Pachymetopon aeneum* also needs to be addressed as these are important components of both the recreational and commercial linefisheries.

At present, there appears to be no "perfect" gear suitable for a panga directed fishery. Otter trawling is non-selective and will possibly have the highest incidence of bycatch and the retainment of juvenile fish due to the clogging effect of long or large trawls. Rod/handlining or longlining with hooks are two possibilities as the technology is well developed in South Africa. The problem of high bycatch using hook-and-line methods needs to be carefully monitored.

## Conclusions and recommendations

The results presented in this thesis contribute towards the sustainable management of panga on the Agulhas Bank. This was achieved by modifying a management procedure (*cf.* Punt, 1993b) developed to manage fish resources that are subjected to directed fishing effort. Inherent problems associated with bycatch assessment and management such as the lack of biological, *CPUE* and other auxiliary fisheries data were investigated. The updated management procedure addressed the relative merits of available data sources and what relevant data should be collected to provide suitable management advice.

A comprehensive study of the life history of the panga was undertaken and those life history parameters necessary for describing the dynamics of the population were estimated. Growth analysis based on sectioned sagittal otoliths revealed that the panga was a slow growing fish with a relatively low rate of natural mortality. This is very similar to other temperate sparid species. Confusion regarding its intersexuality was clarified using detailed histological examination. The panga is a late gonochorist with males and females maturing after a non-functional intersexual stage. After maturation, fish spawned throughout the year. Panga was shown to be an opportunistic benthic predator, exhibiting an ontogenetic shift in diet. This allows it to inhabit extensive areas of the Agulhas Bank.

Further information regarding the spatial dynamic of its distribution and abundance were obtained through the development of a Geographical Information System. It revealed that a nursery area for immature fish exists on the Central Agulhas Bank. After sexual maturation, approximately 40% of the biomass migrated eastwards, colonising large areas of the Eastern Agulhas Bank.

Management options were obtained based on the application of per-recruit and age-structured production models. A preliminary risk analysis was used to assess the sustainability of various catch scenarios. These investigations suggest that panga can be fished at higher levels.

The potential for higher panga catches led to the consideration of a possible directed fishery for the resource. The issue of possible bycatch within a panga directed fishery was investigated. It was shown that those areas which are known to be dominated by panga, such as the large areas of hard ground over the Agulhas Bank, also support a large multispecies fish assemblage. Current methods to catch panga were shown to be unsuitable and creative ways need to be sought by scientists and fishers in designing gears that will selectively target this species, whilst simultaneously reducing excessive bycatch. Furthermore, given that the nursery area of this species is on the Central Agulhas Bank, directed fishing in this area should be restricted. This would alleviate fishing effort on immature fish. Therefore, until suitable methods to direct effort on the panga stock have been developed, this species should continue to be harvested as a bycatch resource.

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